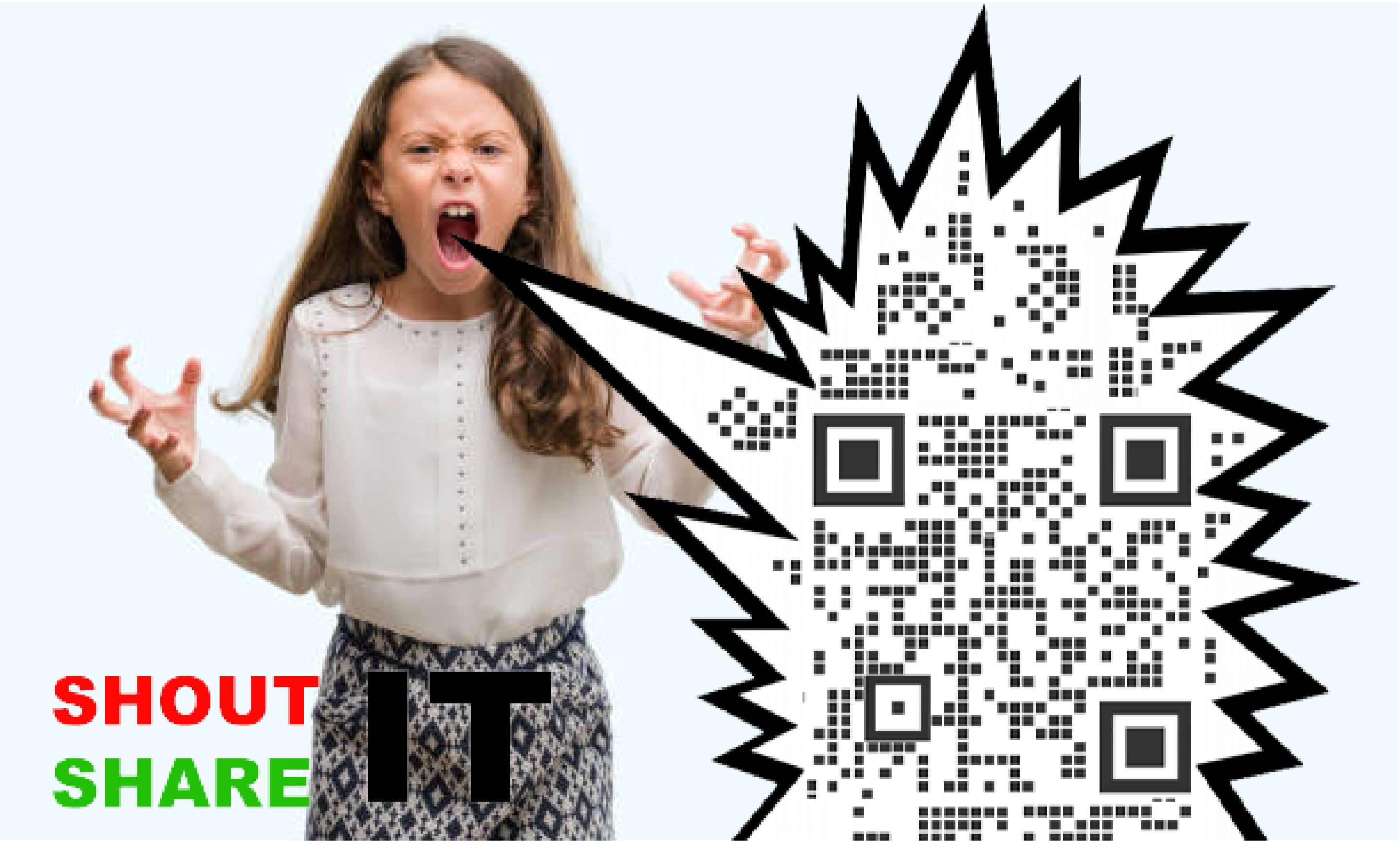
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FOSSIL DENTICIPITID FISHES FROM EAST AFRICA

BRITISH MUSEUM
23 NOV 1960
NATURAL HISTORY

P. H. GREENWOOD

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23 NOV 1960
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BY

PETER HUMPHRY GREENWOOD
Department of Zoology, British Museum (Natural History).

Pp. 1–11 ; *Pls.* 1–3 ; 2 *Text-figures*

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Issued November, 1960 *Price Seven Shillings and Sixpence*

FOSSIL DENTICIPITID FISHES FROM EAST AFRICA

By P. H. GREENWOOD

SYNOPSIS

Recently, a new and distinctive family of small and primitive isospondylous fishes (Denticipitidae) was described from a living population in West Africa. Fossil representatives of this family have now been found in presumed Tertiary deposits near Mahenge, Tanganyika Territory. The living and fossil fishes are closely related but generically distinct; a new and monotypic genus (*Palaeodenticeps tanganikae*) is created for the fossils. Other fish remains, predominantly Cichlidae, from the same deposits are described and discussed.

INTRODUCTION

Some months ago I was asked to study a collection of fossil fishes from Mahenge in the Singida district of Tanganyika Territory. The age of the deposits is unknown but judging from some of the fishes present, it is probably of middle to late Tertiary age. This conclusion is in accordance with geological evidence from the sediments in which the specimens were found (Dr. G. Mannard, *in litt.*).

Amongst the fishes were a number of small specimens whose identity was a complete puzzle except that they were clearly Isospondyli of a clupeoid type. Various characters especially the denticulate cranial bones appeared to be unique and precluded the identification of the fishes with any known family of living or extinct Isospondyli.

This dilemma was solved recently by the publication of a paper describing a new family, Denticipitidae, of extant but primitive clupeoid fishes from rivers in western Nigeria (Clausen, 1959). The degree of resemblance between these fishes and the fossils is so remarkably close, that what differences there are can only be considered of generic value.

MATERIAL

The fossils are in the form of imprints left in lacustrine shales which have preserved the finest details of bone form and ornamentation.

Eight specimens are referable to the Denticipitidae, the majority being entire or almost entire skeletons still naturally articulated. Only one specimen is disarticulated and dispersed, although all have the posterior part of the skull somewhat crushed. The registration numbers given throughout are those of the Department of Palaeontology, British Museum (Nat. Hist.).

(1) Entire skeleton, well preserved. Standard length, 28 mm., total length (measured from snout tip to the posterior tip of the upper caudal lobe) about 32 mm. Holotype of the species: P. 42610.

(2) Entire skeleton, well preserved. S.L., 28 mm., T.L. 32 mm. Although the finer osteological detail is less obvious in this specimen, there is a very clear imprint of the swim-bladder ; also, the structure of the caudal fin skeleton is clearer than in (1). P. 42611.

(3) Distorted and incomplete skeleton. S. L. about 28 mm. P. 42612.

(4) A well-preserved and almost complete skeleton lacking the anterior region of the skull and part of the anal fin. S.L. about 28 mm. P. 42613.

(5) and (6) Two specimens, one on each face of a piece of shale ; both are incomplete skeletons rather poorly preserved. P. 42614 and P. 42615.

(7) A very badly preserved but almost entire skeleton of a fish about 25 mm. S.L. P. 42616.

(8) Part of the trunk and caudal skeleton (including the dorsal and anal fins) from a fish about 25 mm. S.L. ; moderately preserved. P. 42617.

The descriptions which follow are based mainly on specimens (1) and (2) but some additional data were obtained from (3) and (4). The study and interpretation of this material was greatly facilitated by the use of " Silastomer " casts which gave a positive mould of the negative impression. From these casts it is possible to determine the extent and distribution of the finest cranial denticulations, as well as many other delicate structures in the cranial and axial skeleton. I am greatly indebted to Messrs. M. J. Meade and H. K. Ward of the Department of Palaeontology for their skilful preparation of the casts.

THE FAMILY DENTICIPITIDAE

The most outstanding characteristic of the Denticipitidae is, as the name implies, the presence of numerous extra-oral denticles on most dermal skull bones, on the dorsal part of the secondary pectoral girdle and on the scales around the anterior end of the lateral line (see Clausen, 1959 and Text-fig. 1). As far as skull denticulation is concerned, almost complete similarity exists between the fossils and the living species *Denticeps clupeoides*. Compression of the hinder end of the skull in the fossils makes it impossible to determine the dorsal elements of the pectoral girdle series. Consequently, this region could not be studied.

The few and slight differences which do occur in the skull denticulation of the two forms are principally : (i) the presence in the fossils of denticles on the suboperculum and (ii) fewer tooth rows on the lateral face of the maxilla and mandible, there being one less row on each bone. However, since these points can be checked in only two specimens and because nothing is known about the variability of such characters in living fishes, the taxonomic value of these differences cannot be assessed.

Despite careful search I am unable to find denticles on any scale impression, but, as the impressions are weak this difference also should not be given undue importance.

More significant differences noted in the fossils are : fewer vertebrae (31 or 32 cf. 40 in *Denticeps*) and lateral line scales (32 or 33 cf. 37 or 38) dorsal fin arising above the origin of the anal (and not more posteriorly as in *Denticeps*) ; more principal branched caudal rays (20 cf. 18).

These differences are slight when compared with the otherwise great similarity that exists between every verifiable osteological character in the two forms. Unfortunately, the nature of the impressions precludes the study of median structures in the cranium (especially the relation between the supraoccipitals and parietals, and the shape of the nasal and parietal bones) nor is it possible to investigate the nature of the auditory fenestra. The large posttemporal foramen in *Denticeps* does appear to be developed in the fossils and is visible despite compression and distortion.

Clausen (1959) lays particular emphasis on the unique opercular lateral line system of *Denticeps*. The operculum carries from five to seven major sensory canals derived from the posttemporal-extrascapular and infraorbital-preopercular branches of the head. The canals are superficial, uncovered by bone and run obliquely across the bone in a postero-ventral direction. Each canal is fringed by rows of teeth. Naturally, such delicate structures are not well-preserved in the fossils. Nevertheless I believe that in two specimens the course of these canals is faintly visible. In these specimens there are two large toothed areas on the operculum, one situated dorsally and the other, larger area, occupying the antero-ventral angle of the bone (see Pl. 2). In both areas the teeth are arranged in orderly and approximately parallel lines running obliquely downwards and backwards ; the lower group slopes less steeply

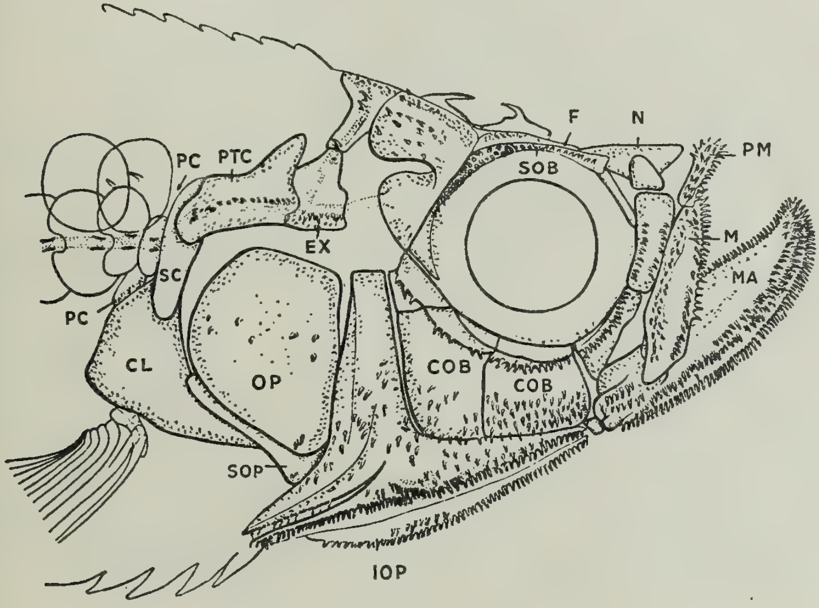

Fig 1. *Denticeps clupeoides* Clausen

Drawing of the syncranium and associated structures showing the superficial bones and the distribution of the dermal denticles ; prepared from an alizarin specimen. In fresh specimens the denticles on the operculum and on the scales are more numerous. (After Clausen, 1959.) For abbreviations, see Text-fig. 2.

than the upper. The position and distribution of these teeth correspond to those fringing the canals in *Denticeps*.

Both *Denticeps* and the fossils have virtually identical caudal skeletons ; as Clausen remarks, the caudal fin must be described as hemi-homocercal. A peculiar feature of the caudal is the presence of a comb-like group of three or four short, unbranched and detached rays which immediately precede the upper and lower caudal lobes. Laterally, the rays are supported by a band of narrow scales. The fossils show this character very clearly (see Pl. 3). The one difference I can find in the caudal skeleton is that only the last two vertebrae are curved upwards in the fossils whereas in *Denticeps* the last four to six vertebrae are involved. Finer details in the caudal osteology of the fossils are not easily discernible, but from observations on three specimens I should doubt whether a distinct urostyle is developed ; the last vertebra is short and compact, and the ultimate uroneural does not extend beyond its posterior limits. Clausen (1959) mentions a urostyle in *Denticeps* but from his photograph of the caudal skeleton in an alizarin preparation, the situation would appear identical with that of the fossils.

One other familial character may be noted here, namely the postcleithrum. In *Denticeps* there are upper and lower postcleithra, both resembling dermal body scales and lying mesially to the shoulder girdle ; the upper postcleithrum is pierced by the main lateral line tube. It is impossible to give a detailed description of the postcleithrum in the fossils because it is largely obscured by the cleithrum ; only the ventral part is visible as a long, slender and postero-ventrally directed rod lying mesially to the cleithrum. No fine details are preserved and any dorsal relations with the lateral line system are obliterated by the crushed posterior part of the skull and upper girdle elements.

Considering the differences known to exist between the fossil and living Denticipidae, it seems reasonable to recognize the former as a separate genus. Certainly, when equated with the differentiae used in classifying present-day African fishes, these differences cannot be considered to have more than generic value.

Genus ***PALAEODENTICEPS*** nov.

Diagnosis. A member of the family Denticipitidae, differing from the extant genus *Denticeps* in having fewer vertebrae (31 or 32 cf. 40) and lateral line scales (32 or 33 cf. 37 or 38) ; origin of dorsal fin above or slightly anterior to first anal fin ray, suboperculum with numerous small denticles, caudal fin with 20 (cf. 18) principal branched rays.

Type species. *P. tanganikae* sp. nov.

Palaeodenticeps tanganikae sp. nov.

(Pl. 1–3 ; Text-fig. 2)

Diagnosis. As for the genus.

Holotype. A specimen about 28 mm. standard length. P. 42610.

Locality. Lacustrine shales near the western margin of the Iramba Plateau, Singida district, Tanganyika Territory.

AGE. Uncertain but probably middle to late Tertiary.

DESCRIPTION. In general appearance, *Palaeodenticeps* bears a striking resemblance to *Denticeps*. This overall similarity extends to a number of osteological characters (see above).

The scales along the dorsal mid-line form a clearly demarcated ridge and there is a distinct line of keeled scutes along the belly ; about twenty scutes, extending from the level of the posterior preopercular margin to a short distance from the anal fin, form this ventral keel. The first ten pairs of ribs are intimately united with the scutes but the last three pairs are apparently free ventrally.

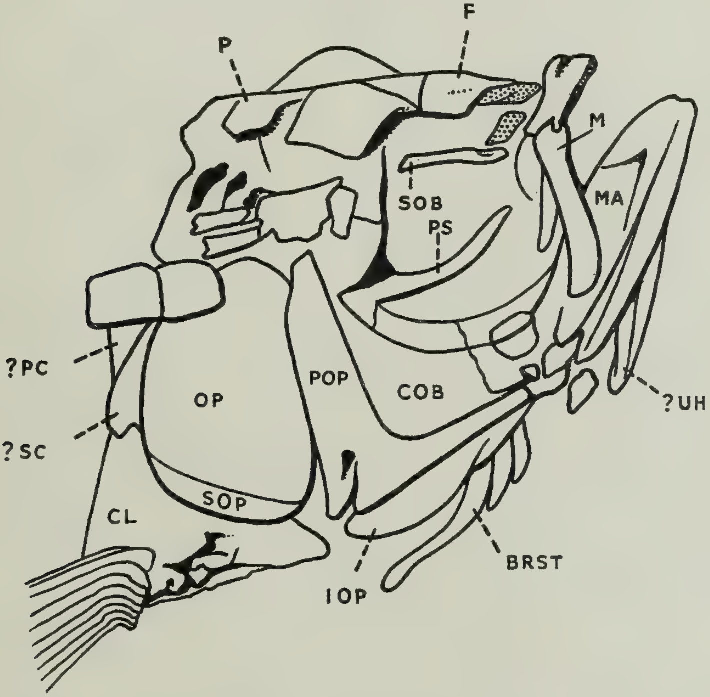

FIG. 2. *Palaeodenticeps tanganikae* sp. nov. Outline drawing of the syncranium, from the holotype (× 10). P. 42610.

BRST., branchiostegal rays ; CL., cleithrum ; COB., circumorbitals ; EX., extrascapula ; F., frontal ; IOP., interoperculum ; M., maxilla ; N., nasal ; OP., operculum P., parietal ; PC., postcleithrum ; PM., premaxilla ; POP., preoperculum ; PS., parasphenoid ; PT., posttemporal ; SC., supracleithrum ; SOB., supraorbital ; SOP., suboperculum ; ?UH., urohyal (?)

As in *Denticeps*, the postero-ventral angle of the preoperculum is divided and forms a double projection fringed with denticles. Slightly posterior to the base of the division, there is a round depression which resembles an opening to the lateral line tube. No such pore is mentioned or figured in the description of *Denticeps*. The divided angle of the preoperculum is not markedly protracted in *Palaeodenticeps* ;

in *Denticeps* it forms a double spine extending to a point below the posterior margin of the operculum (cf. Text-fig. 1 and Plate 2). Possibly, the spinous portion has been broken off in the fossils.

As mentioned above, the suboperculum carries scattered denticles. The interoperculum, like that of *Denticeps*, is toothed and pointed posteriorly ; it appears to be stouter in *Palaeodenticeps* than in the extant genus. There are four or five, broad and stout branchiostegal rays ; it is impossible to ascertain whether, as in *Denticeps*, the median pair is toothed.

No obvious differences could be detected in the circumorbital series of the two genera ; the conspicuous, comb-like supraobital of *Denticeps* does seem to be present in the fossils but this point needs confirmation.

In general, the lateral aspects of the pectoral girdle are alike in both genera but it is still unknown whether, as in *Denticeps*, there are two rows of pectoral radialia in *Palaeodenticeps*. The fin itself occupies a similar position, but the tip extends relatively more posteriorly in *Palaeodenticeps* where it reaches to the level of the ventral fin origin ; there are nine pectoral rays in this genus. The ventral fins are poorly preserved in all the specimens and it is impossible to count the number of rays, except in so far as there are at least five and probably not more than eight.

The lateral line canal of the flanks is complete and extends from behind the cleithrum to the extremity of the caudal peduncle. It follows a gently curved course, situated midway between the dorsal and ventral body outlines. There are 32 or 33 scales in the lateral line series (counted in two specimens).

Apart from the total number of vertebrae and the number of up-turned vertebrae involved in the caudal fin skeleton (see above) there is little difference between the axial skeletons of the two genera. Faint traces of epineural and epicentral bones can be detected in two specimens, but the evidence for the presence of epipleurals is less definite. Dorso-spinal bones (i.e. elements apparently homologous with the dorsal pterygiophores but not bearing fin rays) are present above each of at least the first twelve vertebrae (that is, two more than in *Denticeps*).

The anal fin is long and low, comprising 24 or 25 branched rays ; in the two specimens with entire anals there are three unbranched, unsegmented spine-like rays preceding the branched rays, thus giving a total fin ray count of 27 and 28. The dorsal fin is short and comprises eight rays (counted in three specimens) ; the first ray may be unbranched but apart from this possibility and its greater length, it is in no way different from the others. In some specimens, the branched parts of the dorsal rays appear to be very pliable and almost filamentous (judging from the way in which the distal ends of the rays have been thrown into curves). Other specimens seem to have more rigid tips to the dorsal rays, but this may merely be due to the vagaries of preservation.

One specimen (P. 42611) is particularly well preserved with little distortion or disarticulation. From this fish I have made a number of measurements, tabulated below. The fixed points used to obtain these measurements are, as far as possible, those used by Clausen (1959) to describe *Denticeps clupeoides*. Exceptions are marked with an asterisk (taken from the anterior tip of the premaxilla and *not* the mid-point of the upper jaw between the premaxillae) ; those marked with a dagger are taken from the lateral end of the premaxilla and thus accord with Clausen's practice.

	mm.	% S.L.
Standard length	28·0	—
†Length of head	6·0	21·5
Depth of body	9·0	32·2
†Length of snout	1·3	4·7
Length of orbit	3·0	10·7
Postorbital head length	3·0	10·7
*Snout to 1st dorsal ray	17·0	60·8
†Snout to 1st anal ray	17·5	62·5
†Snout to pectoral insertion	6·0	21·4
†Snout to pelvic insertion	13·0	46·5
Pectoral to pelvic insertions	7·0	25·0
Length of dorsal fin at base	3·0	10·7
Length of anal fin at base	8·0	28·6
Caudal peduncle : Length	5·0	17·8
Depth	4·0	14·3

ECOLOGY

Dr. G. W. Mannard of McGill University, who is studying the Singida deposits, has kindly informed me of his preliminary conclusions. He writes " These sediments are lacustrine shales which fill a depression in an area of granite near the western margin of the Iramba Plateau of central Tanganyika. The structure and heavy mineral content of the shales suggest that they are crater lake deposits over a kimberlite pipe ". If *Palaeodenticeps tanganikae* inhabited crater lakes, then its ecology differed considerably from the extant *Denticeps clupeoides*. This species is fluviatile and occurs in " fast-running, medium-sized streams of low mineral content " (Clausen, 1959). However, the ecological evidence for the fossils is too scanty to be considered conclusive, especially since the evidence furnished by associated fishes (see below) neither confirms nor contradicts it.

DISCUSSION

The Denticipitidae, both living and fossil, provide an intriguing puzzle. Clausen (1959) considers the relationships of the family with various isospondylous families and finds characters in common with the Elopidae, Albulidae and Clupeidae (all of the suborder Clupeoidei) as well as with Osteoglossidae (Osteoglossoidei). In addition, there are characters not found in any of these families or either suborder, as, for example, the denticulate dermal bones of the head. Indeed, the only other fishes with such extensive extra-oral cephalic dentition are those of the genus *Atherion* (Atherinidae, Mugiloidei, see Rofen, 1958), which are phyletically far removed from the Denticipitidae. As Dr. Clausen is still studying the anatomy of *Denticeps* I am unwilling to carry this discussion further. It must suffice to say that wherever the relevant characters are preserved in the fossils I have been able to confirm most of his observations ; from Clausen's published account and my own observations I would suspect that the Denticipitidae represent a group of subordinal status within the Isospondyli.

The known distribution of the family, with the fossil genus in the east (Tanganyika) and the extant *Denticeps* in the west (Nigeria), is unusual ; no other family of African freshwater fishes is restricted to such widely isolated areas. Further collecting may show that the living forms have a wider distribution and thus narrow the present geographical gap. Nevertheless the Denticipitidae do provide additional support for the concept of a once widespread, possibly pan-African, and relatively uniform ichthyofauna during the late Tertiary and early Quaternary periods. Evidence already available (Greenwood, 1951, 1959) shows that this was the condition over a relatively restricted area in East Africa where today there are at least three distinct faunal units.

THE FISH-FAUNA ASSOCIATED WITH *PALAEODENTICEPS*

At least two other families are present in the Singida collection. One of these is unidentifiable from the impressions preserved. The fishes represented are moderately large ; one almost complete vertebral column is from a fish about 10 cm. long. Other unidentifiable material consists of isolated vertebrae, ribs and fin rays. None of these specimens is as well preserved as the *Palaeodenticeps* specimens or those of the other and identifiable family, the Cichlidae.

Thirteen specimens, all negative impressions and all referable to the same genus can be identified as cichlids (P. 42602–09 and P. 42618–22). Unfortunately, no entire skeletons are preserved, but from various fragments it has been possible to reconstruct several of the more important taxonomic characters.

The Cichlidae are widespread in Africa, and represented by numerous genera and species notorious for their complex and often difficult taxonomy. The really trenchant generic characters are found in the cranial osteology and in the pharyngeal dentition. None of these characters is preserved in the fossils so it has been necessary to rely on secondary characters such as scale types, number of vertebrae, fin ray counts and the oral dentition.

In a few specimens there are clear impressions of relatively stout and unicuspid teeth on the premaxilla and dentary ; the teeth are not numerous in either jaw. Where scale impressions are present it is obvious that the scales are ctenoid. Taken together, these characters virtually eliminate the possibility of these fishes being *Tilapia*, one of the genera likely to be present in this region.

The low number of vertebrae (about 28) and the number of dorsal fin rays (15 spines + 9 branched rays) also reduced the possibility of these specimens being *Tilapia*. The sum of these characters, on the other hand, strongly suggests the genus *Haplochromis*, an ubiquitous genus distributed throughout Africa. The same characters, together with the general facies of the few almost entire specimens suggest close affinities with the extant *H. bloyeti* (Sauv.) and *H. wingati* (Blgr.), especially the former. The resemblance is not exact, but because of the difficulties in differentiating species of living *Haplochromis* I do not consider that any advantage would acrue from describing the fossils as a distinct species. *Haplochromis bloyeti* (which occurs in the streams and rivers of present-day Tanganyika) has a wide ecological tolerance, as have most of the living generalized and fluviatile species. It would not be unreasonable to assume the same characteristics for the earlier species, which cannot therefore provide any critical information on the ecological conditions at the time preceding their death.

The earliest record of fossil Cichlidae in Africa is from Miocene deposits on Rusinga Island in Lake Victoria (Greenwood, 1951). Fishes from these beds share some characters with those from Singida, notably the small size, similar fin ray counts and a low number of vertebrae. Since the teeth and scales of the Rusinga fishes were not well preserved no generic identification could be made with certainty. Although I suggested that these fishes might be *Tilapia* (Greenwood, 1951), further material examined by Dr. Ethelwynn Trewavas indicates that some could be referred to *Haplochromis* or even to *Pelmatochromis* on the characters preserved (Trewavas, 1957, unpublished report). The identity of the Singida cichlids is certainly more definite.

ACKNOWLEDGMENTS

It is with great pleasure that I thank Dr. G. W. Mannard and Dr. H. S. Clausen who have discussed with me their unpublished researches on, respectively, the deposits and the living fishes ; my thanks are also due to Dr. E. I. White, Keeper of Palaeontology, who read and criticized the manuscript of this paper.

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BRITISH MUSEUM NATURAL HISTORY

PLATE 1

Palaeodenticeps tanganikae sp. nov. Cast of the holotype. × 5. With respect to plates 2 and 3 the lighting is reversed.

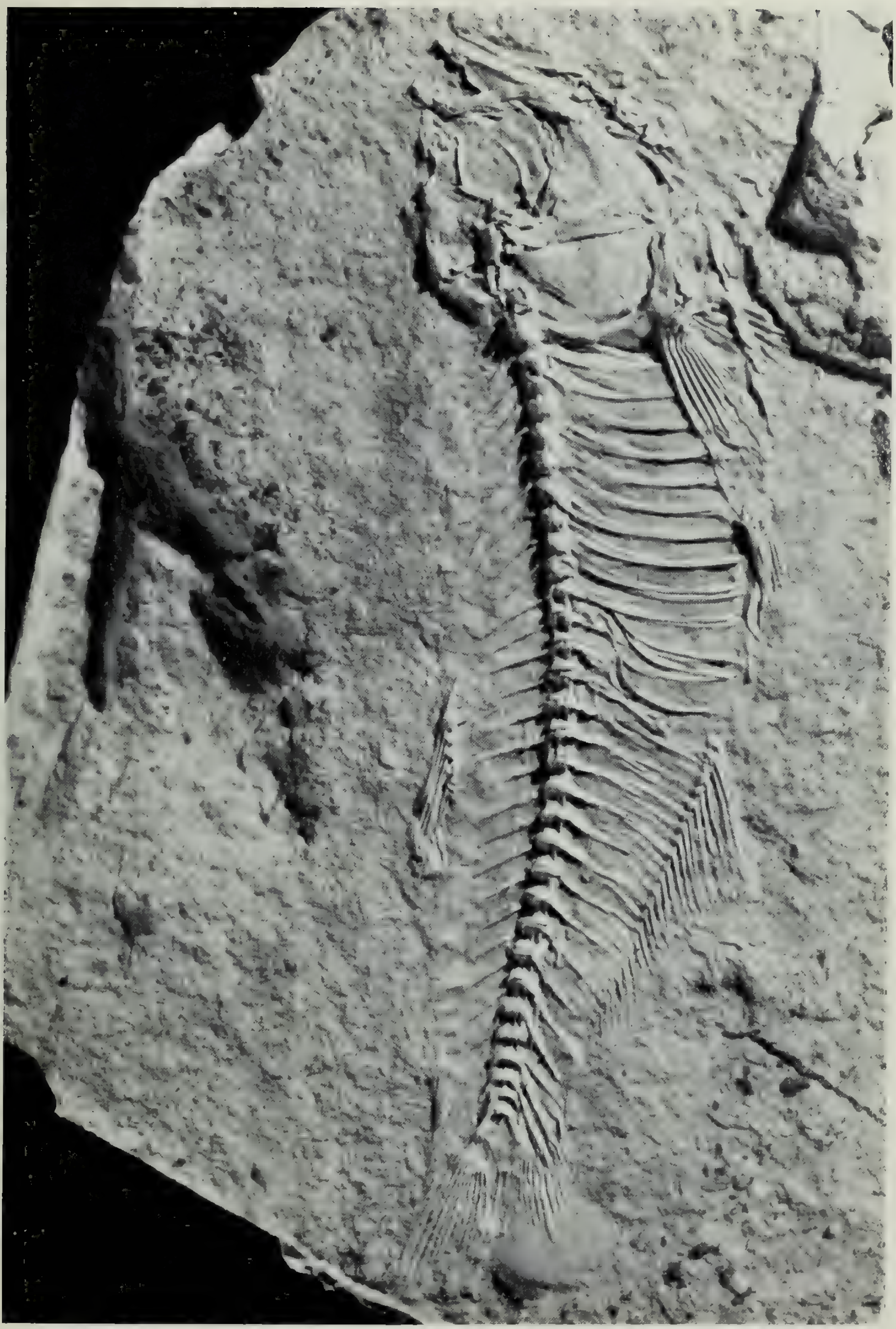


PLATE 2

Palaeodenticeps tanganikae sp. nov. Cast of the holotype. × 10.

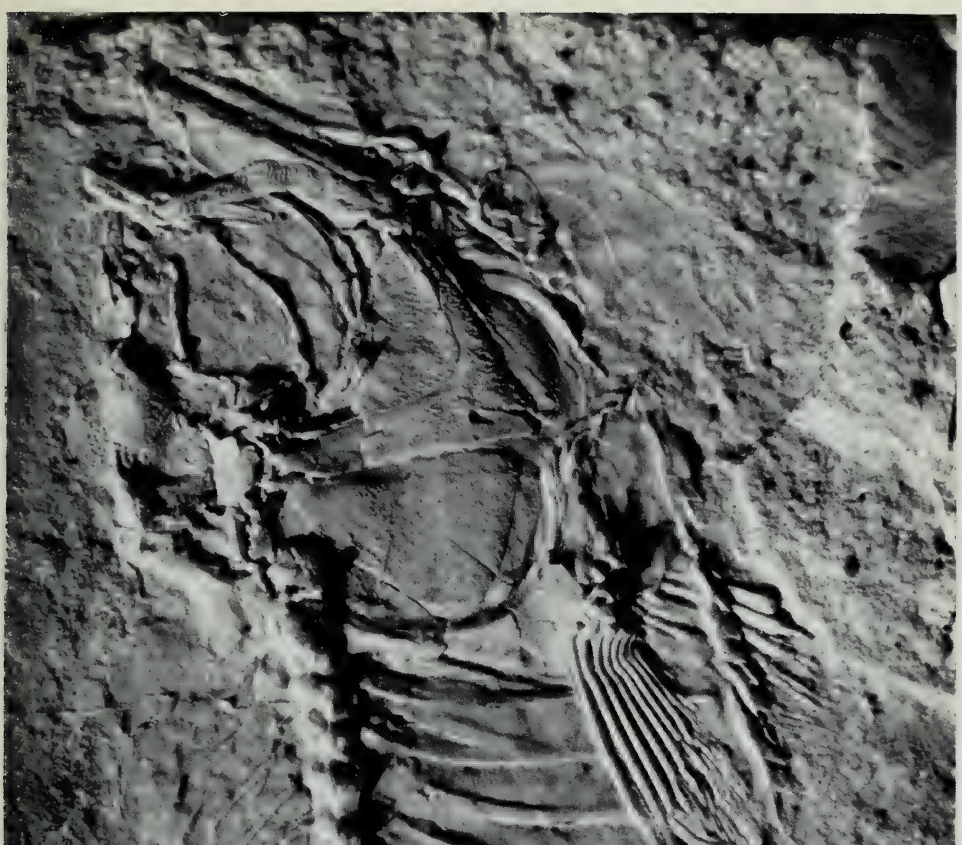
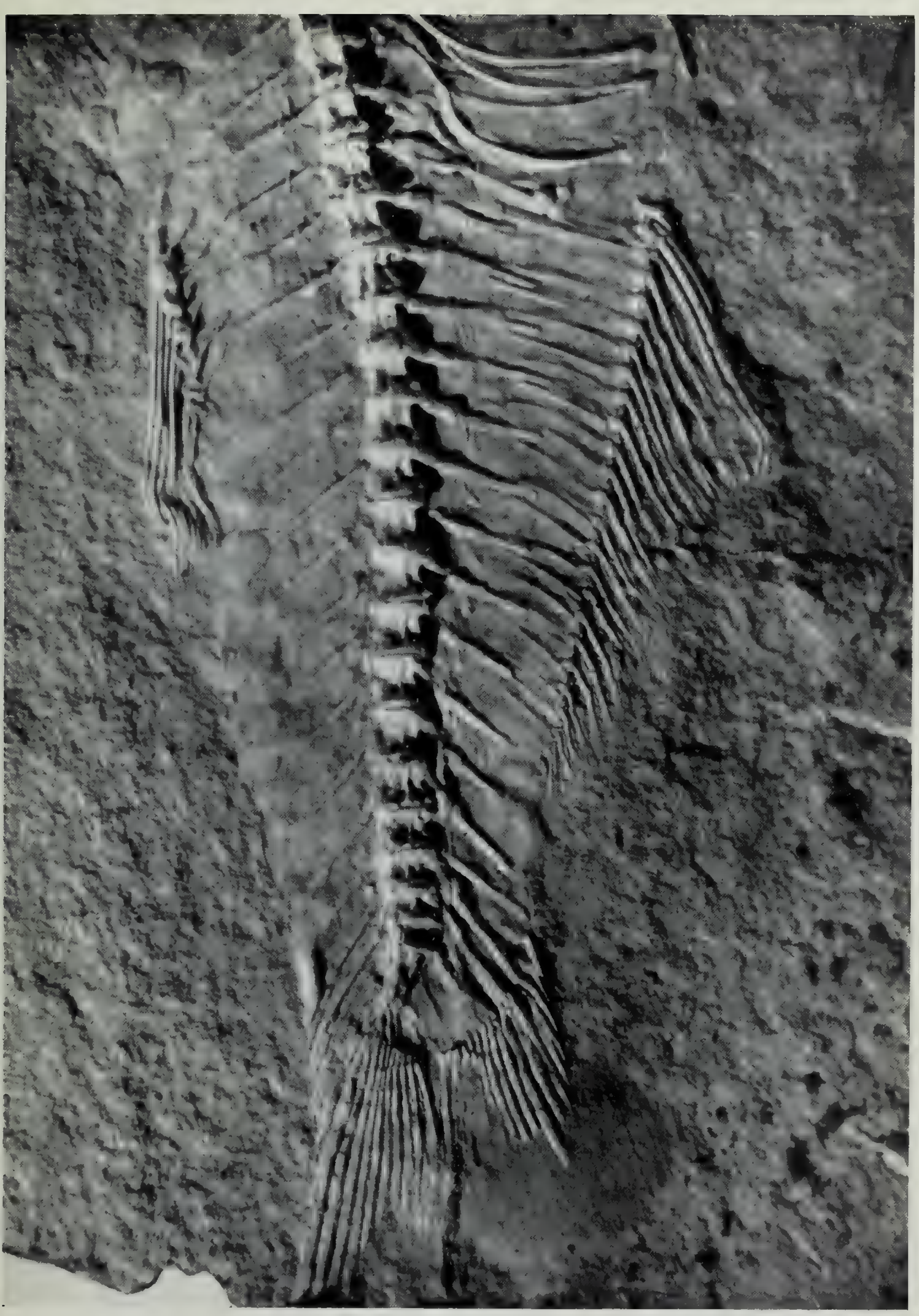


PLATE 3

Palaeodenticeps tanganikae sp. nov. Cast of the holotype. × 10.



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POST-YPRESIAN PLANT REMAINS FROM THE ISLE OF WIGHT AND THE SELSEY PENINSULA, SUSSEX

M. E. J. CHANDLER

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POST-YPRESIAN PLANT REMAINS FROM THE ISLE OF WIGHT AND THE SELSEY PENINSULA, SUSSEX

BY

MARJORIE E. J. CHANDLER

Pp. 13–41 ; *Pls.* 4–11

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POST-YPRESIAN PLANT REMAINS FROM THE ISLE OF WIGHT AND THE SELSEY PENINSULA, SUSSEX

By M. E. J. CHANDLER

SYNOPSIS

The larger geographical features which are the background of post-Ypresian plant life in the Hampshire Basin are indicated. Marine dated deposits in the east of the Basin are seen as related to continental deposits in the west. In the marine beds there is a scarcity of plants, partly no doubt owing to the distance from the land surface on which they grew, partly to the narrow outcrop of the strata. Two marine areas, Whitecliff Bay, Isle of Wight, and Selsey, Sussex, are considered. The former has yielded only one determinable plant up to date, a *Limnocarpus* in Cuisian Beds. The Selsey area with its variable beds and tropical or subtropical fauna has yielded a few species in part at least of Poltavian type. Reference is made to published descriptions of the deposits by Fisher, Reid, Wrigley & Davis and Curry.

INTRODUCTION

In studying the fossil plants of the Hampshire Basin it is helpful to have in mind some general picture of the larger geographical features of the period. In post-Ypresian times evidence of various kinds indicates a continental area to the west with a river system which debouched into a sea lying to the east. Tidal swamps occurred at various points as denoted by beds of *Acrostichum lanzeanum*. They have been found on the present-day coast at Studland and Arne (Dorset), Bournemouth and Hordle (Hampshire).

The massive freshwater Lower Bagshot Beds of Dorset and Middle Bagshot of Dorset and west Hampshire (to use Gardner's familiar terms for the Dorset Pipe-clay Series and Bournemouth Freshwater Beds respectively) and the succeeding brackish estuarine beds with coastal shingle banks of the Bournemouth Marine Series were deposited in the continental region while contemporary marine beds were being formed further to the east. For suggested correlation of the deposits of the two areas by Wrigley & Davis and by Arkell see Chandler (1960*a*, Table on p. 8).

The marine beds are now exposed at the eastern end of the Isle of Wight and in the coast section on both sides of the Selsey peninsula. As might be expected from its position midway between Bournemouth and Sussex the Isle of Wight displays non-marine beds at its western end, well seen at Alum Bay but with a little known flora, and marine beds at its eastern end visible in Whitecliff Bay. Accounts of the fossil plants of the continental western area await publication in a number of monographs and bulletins of the British Museum (Natural History). A consideration of the plant remains of the marine eastern area follows below.

PLANT REMAINS IN THE MARINE BEDS

Although the marine beds were laid down in the sea, or at least at the seaward end of an estuary with marine currents, the land was near enough for plant remains to drift from it to the localities under consideration before they became water-logged to sink and be buried among the marine detritus. Yet it was sufficiently remote for such remains to be scarce. Moreover land mollusca appear so far to be absent altogether while according to Reid (1897 : 8) evidence of only one land mammal has been found. The sparse plant remains include scanty evidence of a true land flora (*Araucarites, Laurocalyx, Wetherellia*) together with estuarine or riparian plants (*Limnocarpus, Caricoidea*) and *Nipa* from tidal mud swamps.

Although so little of the contemporary flora has survived, that little is important because the beds are well dated by marine organisms including *Nummulites* while the range of the strata, Cuisian to Auversian, is wide. In the Isle of Wight younger beds are also exposed but these up to the present have not yielded determinable plant remains although sifting may yet reveal some. It must be borne in mind that the habitats of the plants in both the continental and marine areas are in the same land mass, so that the dated plants of the marine beds represent the impoverished relics of a rich contemporary flora only vaguely dated where found in the continental beds. Possibly in time to come plants from the dated marine area may help in the more exact correlation of the continental plant beds, for although macrofossils are at present few, pollen may yet contribute to this end and additional plant débris of a larger kind may reward persistent search. Hence to stimulate interest in collecting plants from the marine area is most desirable although the limited outcrop of successive horizons at Selsey makes such collecting an arduous task calling for long-term effort.

A. *A Solitary Plant,* Limnocarpus, *in Cuisian Beds at Whitecliff Bay, Isle of Wight*

The Whitecliff Bay section was described in some detail by Fisher (1862 : 65). He numbered successive beds of the Bracklesham Series there with Roman numerals. The section was again examined by Wrigley & Davis (1937 : 205) who used Fisher's Roman numerals on which they superimposed their own Arabic numbering of subdivisions. These Bracklesham Beds include Cuisian, Lutetian and Auversian horizons. At horizon 1 of Fisher Bed IV a solitary endocarp of ?*Limnocarpus forbesi* (Heer) was found by A. G. Davis. It is the only identifiable plant yet found and is the earliest record of a species which, under the name *Limnocarpus headonensis* (Gardner) is abundant in the Bournemouth Marine and later Eocene and Oligocene beds. Fisher Bed IV yields a fauna of Cuisian age including *Nummulites planulatus*. Wrigley & Davis suggested that the Lower Bagshot Beds and the succeeding lowest Bracklesham, Fisher Beds I to III which they regarded as azoic, may be non-marine (1937 : 205, 219). This opinion Mr. Curry writes (personal note) is doubtful because there are moulds of probably marine mollusca in Bed I, and a band of well-rolled flints at its base. It is necessary here to place on record that Mr. Curry has kindly read this manuscript and made many helpful criticisms together with most generous and valuable contributions from his great knowledge of the Bracklesham localities. Wrigley & Davis placed Fisher Bed IV at the top of the Cuisian although they stated that the precise upper limits of this stage are obscure. They suggested that Fisher Bed III, where lignitic seams occur (1937 : 219) may yield plants as some seeds have been found in these seams. Unfortunately these seeds have not been traced.

B. *Plant-bearing Beds of the Selsey Peninsula* (*Cuisian to Auversian*)

The Bracklesham Series at Selsey is very variable and yields a prolific fauna said to be of distinctly more tropical aspect than that of the London Clay. According to Gardner (1882 : 472) the animals are those of a tropical sea which extended south over the Paris-Belgian Basin with southern limits just south of Paris and western perhaps near Evreux. Reid (1897) reiterates the variability of the series with its fauna of tropical and subtropical aspect.

The classic account of the beds by Osmond Fisher is in the same paper as his description of the Whitecliff Bay sequence and there is some comparison and equating (albeit erroneous, Mr. Curry states) of the two localities. Only the horizons which outcrop along the shore between the Bracklesham Bay Hotel and Selsey Bill and again on the east side of the peninsula were known to Fisher who recorded that the lowest beds (i.e. those north-west of the Hotel towards Chichester Harbour) were covered at that time (Fisher, 1862 : 76). The successive horizons which he did examine were denoted by Arabic numerals still in use but he thought, incorrectly it appears, that these beds spanned approximately the same period as the Bracklesham Beds of the Whitecliff Bay section. In 1937 Wrigley & Davis demonstrated that the lower part of the Bracklesham Beds of the Selsey area (those, that is, unknown to Fisher) were of Cuisian age. They succeed the fine-grained marine sediments of the London Clay and were named the Cakeham Beds by Wrigley & Davis who divided them into a Series A below formed of grey quartzose sands equivalent to the Lower Bagshot of Whitecliff Bay and a Series B above formed of sandy clay with a Cuisian fauna including *Nummulites planulatus* and equivalent to Fisher Bed IV of Whitecliff Bay. Fisher himself (1862 : 93) had equated his Bed 1 of Bracklesham with Bed IV of Whitecliff Bay. A recent Excursion Handbook by Curry & Wisden (1958) is of great practical help to anyone studying the Section and gives an excellent up-to-date summary of the successive beds and their positions in the foreshore. It is unnecessary to repeat here details already published by the various workers except as far as may be necessary to explain the age of the plants. As at Whitecliff Bay the Bracklesham Beds include deposits of Cuisian, Lutetian and Auversian age.

The exposures are between tide marks so that collecting is most satisfactory at low water of spring tides as the greatest area is then uncovered (Curry & Wisden, 1958 : 13) but at any time the section or parts of it are liable to be obscured by beach sand to a varying degree. Hence the value of constant observation spread over many years which can best be undertaken by local collectors. By such efforts the brief plant list may yet be considerably augmented. In particular it is important that plants *in situ* should be obtained and Mr. Curry, in searching for other fossils, has already made a start by the discovery of plants in washed residues from carefully specified beds.

PLANTS OF THE SELSEY AREA AND THEIR HORIZONS

Whereas long-drifted wood and twigs are not uncommon, Selsey has so far yielded few genera, species, or even (in most cases) individual examples of a particular plant. The majority of finds have been picked up loose on the beach, probably derived from beds near the spots where they were found e.g. loose fruits of *Nipa* from the Palate Bed (see p. 34). A few specimens have been collected *in situ*. In order to show clearly the horizons which have yielded plants, all found up-to-date are listed in the following Table. The first column shows horizon and locality if known, and the finders of the specimens. The second column gives the names of the plants with brief notes and the B.M. (N.H.) registration numbers of extant material.

Cuisian	
Cakeham A Beds. Opposite West Wittering Beacon. C. Reid (1897 : 6), Gardner (letter to Reid undated)	*Nipa burtini* (Brongniart) Large carbonaceous " skins " filled with grey quartzose sand (see Wrigley & Davis, 1937 : 215, footnote). Friable, collapse on drying (see p. 33).
A. G. Davis	*Wetherellia* sp. (? *W. dixoni* (Carruthers)) (V.35718). Large carbonaceous coccus mineral impregnated in coarse grey quartzose sandstone crowded with lignitic fragments (see p. 37).
Cakeham B Beds (Marine Phase). East Wittering. D. Curry	*Scirpus lakensis* Chandler (V.29213). Abraded fruit (see p. 33).
Lignitic Phase between Cuisian and Lutetian (*ex lit.* A. G. Davis)	
Equated by Davis with Fisher Bed V of Whitecliff Bay, Isle of Wight. Laminated clays and lignite. *In situ.* East Wittering. A. G. Davis	*Araucarites selseyensis* n. sp. (V.41918, holotype) and slides of cuticle (V. 41918*a–o*). Detached cone-scale on back of same block (see pp. 23, 26).
Grey clay with leaves. *In situ.* East Wittering. A. G. Davis	*Araucarites selseyensis* (V.41919 and slides V.41919*a–l*). Twig and counterpart embedded in clay (see p. 23).
Grey clay, 10–20 yds. east of Bracklesham Lane. *In situ.* M. Goodchild	*Wetherellia dixoni* (Carruthers) (V. 41923). Fruit (see p. 37).
Lutetian	
Fisher Bed 2 (*Turritella* Bed). From washings. Bracklesham. D. Curry	?*Wetherellia variabilis* Bowerbank (V. 41886). Small coccus (see p. 39).
Fisher Bed 4 (Palate Bed). *In situ* (*ex lit.* D. Curry) and loose on shore. D. Curry, S. D. & L. T. Garner. Also one fruit recorded C. Reid (1897 : 6) loose near channel from Earnley and *Turritella* Beds, presumed therefore to come from Fisher Bed 4	*Nipa burtini* (Brongniart) (V.29214, V.29215, V.32593, V.40260). Fruits (see p. 34).

Probably Fisher Bed 6. Bracklesham Bay. Ferruginous cemented sand block with lignite, glauconite and *Nummulites laevigatus*. S. D. Garner	*Nipa burtini* (V.33732). Minute, immature fruit and unrecognizable poorly preserved seeds (see p. 34).
Near Fisher Bed 7, loose on shore. Bracklesham Bay. D. Curry	*Laurocalyx* sp. (V.41885). Cupule (see p. 35).
Loose on shore, probably from Fisher Bed 7 or 8 certainly Lutetian. D. Curry	*Nipa burtini* (V.35722, V.35743). Including very large carbonaceous fruits (see p. 35).
Fisher Bed 9 (*Ostrea tenera* Bed). *In situ*. D. Curry	*Carpolithus curryi* n.sp. (V.41887). Pyritized imperfect fruit (see p. 39).
ca. LUTETIAN-AUVERSIAN BOUNDARY	
Fisher Bed 11 or 12. Washings of sandy marine clay. D. Curry	*Limnocarpus forbesi* (Heer) (*L. headonensis* (Gardner)) (V.41870–73). Endocarps (see p. 28). *Limnocarpus*(?) *enormis* n.sp. (V. 41874–83). Endocarps (see p. 29). *Caricoidea obscura* Chandler (V.41884). Fruit (see p. 33).
AUVERSIAN	
Fisher Bed 21 or 22. Opposite Medmery Farm (Medmeney of Dixon, Medmerry of Reid, Medmery of Fisher, Wrigley & Davis) at low water in beds with *Nummulites variolarius*. *In situ*. A. G. Davis. (Equated by Davis with Fisher XVII of Whitecliff Bay, Isle of Wight on field label and in Wrigley & Davis, 1937 : 216)	*Araucarites selseyensis*? (slide V.41921). Twig, totally decayed (see p. 26).
Fisher Bed 21 (Hard Bed). From washings, Selsey. D. Curry	*Carpolithus* sp. (V.41888). Valve of endocarp (see p. 40).
Fisher Bed 21. Selsey. D. Curry	Family Potamogetonaceae, Genus? (V. 41922). Rhizome (see p. 30).
FAIRLY LOW IN THE SERIES, TOWARDS THE MIDDLE OF BRACKLESHAM BAY (Gardner, 1886 : 4)	
Dixon (1850 : 84, pl. 9, fig. 3 ; 1878 : 162)	*Pinus dixoni* (Bowerbank). Holotype (decayed) formerly in Botany Dept. B.M. (N.H.). Cones. (see p. 22).
Gardner (1884, pl. 13, figs. 1, 2, 8)	*Pinus dixoni*. Formerly in Sedgwick Museum, Cambridge (now decayed) (see p. 22).
Dixon (1850 : 84, pl. 9, fig. 4 ; 1878 : 163) Gardner (1884 ; pl. 13, fig. 9)	*Pinus bowerbanki* (Carruthers). Holotype decayed. Cones. Formerly Gardner Coll. decayed (see p. 22).
J. J. B. Ogle. Bracklesham Bay, labelled *Pinites Dixoni* Bowerbank	*Pinus bowerbanki* (V.3313). Cone (see p. 23).
HORIZON ?	
Small rolled clay pebble on shore. Bracklesham Bay. E. M. Venables. Thought by finder to be Lutetian	*Araucarites selseyensis* (V.41920*a–j*). Twigs now represented by slides (see p. 23). Family Potamogetonaceae, Genus? (V. 41889–41917). Water plant, buds and vegetative fragments (see p. 31).

Horizon? (Widely distributed loose on beach)

Loose on shore. Bracklesham Bay. Dixon (1850 : 84, pl. 9, fig. 2)	*Wetherellia dixoni* (Carruthers). Carbonaceous fruits variously distorted (see p. 36). V.40509, holotype. Five-carpelled fruit.
Loose. Thought to be Auversian. E. M. Venables	V.33825–26. Two fruits, one six-carpelled.
Loose. Thought to be Lutetian. Mrs. J. G. Turner	V.33827. Seven-carpelled fruit with spine-bases and casts of hollow spines.
Loose. Thought to be Auversian (Brook Bed). Mrs. J. G. Turner	V.29219. An imperfect fruit. V.29218, V.29220. Two perfect fruits showing casts of hollow spines.
Loose. Picked up nearer the Witterings than Thorney, site of Campanile Bed. Thought to be Cuisian possibly or from beds equivalent to Fisher V of Whitecliff Bay. A. G. Davis	V.32591, V.33828.
Loose on shore. N. A. Pye	V.40259. About 100 fruits scattered over a restricted area of Recent sand probably within the span of Fisher Bed 4 to Fisher Bed 7. (Information from D. Curry.) Much water-worn, very variable in size, laterally compressed.

Apart from the records in the above list there is drifted and teredo-bored wood which lies outside the scope of this paper. It may, however, be noted in passing that coniferous wood and palm wood have both been recorded from Bracklesham Bay. Palm wood from Tertiary beds is also known from Bognor and Worthing (Carruthers *in* Dixon, 1878 : 162–167).

Of the Selsey plants *Araucarites*, *Limnocarpus*, *Caricoidea obscura*, *Nipa*, *Wetherellia* and Lauraceae are typical constituents of the Poltavian flora (cf. Chandler, 1960 : 11). *Pinus* occurs in London Clay, Hengistbury and Barton Beds. *Limnocarpus forbesi* (= *L. headonensis*) is highly characteristic of beds above the Bournemouth Freshwater Beds in Hampshire and the Isle of Wight possibly because it is an estuarine plant. Its absence from the older beds of the Bournemouth area may be due to the lack of estuarine conditions rather than to the non-existence of the species at an earlier period. A record by Gardner (1886 : 400) has now been elucidated. He mentioned that in the higher beds the surface was dotted with *Posidonia* " a marine monocotyledonous plant identical with a species now inhabiting the Mediterranean ". Of this plant no figures were given and few words of description, but a recent discovery (p. 30) appears to indicate the presence of a marine monocotyledon of the family Potamogetonaceae although the generic affinity is not yet clear.

1. WHITECLIFF BAY, ISLE OF WIGHT (CUISIAN BEDS)

ANGIOSPERMAE

Class MONOCOTYLEDONES

Family POTAMOGETONACEAE

Genus ***LIMNOCARPUS*** C. Reid emend. Reid & Chandler, 1926 : 68

? ***Limnocarpus forbesi*** (Heer)

(Pl. 7, figs. 20, 21)

For synonyms and history of this species see pp. 28, 29.

DESCRIPTION. *Endocarp* (V.33813) : A subglobose internal cast broken at the style so that the hilar end of the enclosed seed projected through the matrix which was a cast of the locule. Germination valve not represented, its form nevertheless clearly defined by the smooth edges of the locule-cast. It arose at the attachment but its exact limits at the upper end were difficult to distinguish because the locule-cast had split in the plane of symmetry at the apex. Maximum breadth of valve, 0·4 mm. ; length about 1·3 mm. The internal processes on the carpel wall were partly broken so that the corresponding pits on the cast are not preserved, but sufficient remained to show their original position beneath the exposed hilar end of the seed close to the ventral margin towards which they are directed obliquely downwards. Surface of cast smooth, cells obscure apparently about 0·016 mm. in diameter. External surface of endocarp not preserved. Length of endocarp, slightly incomplete, 1·7 mm. ; breadth, 1·3 mm. ; thickness, 1·15 mm.

Seed : Solitary, curved, pendulous. Testa thin, surface smooth, shining, cells indistinguishable, hilum indicated by a small truncation on the upper end of the seed.

REMARKS AND AFFINITIES. One specimen belonging to Potamogetonaceae and to the extinct genus *Limnocarpus*. The characters of the external surface are not known, so that whether or not it was rugose cannot be seen, hence the determination is regarded as provisional. The form and size agree with *L. forbesi* (formerly *L. headonensis*). It closely resembles specimens from Bed K, Bartonian of Barton cliff, Hampshire which are similar smooth locule-casts comparable in every respect but in that case the specific identity is confirmed by the presence of abundant rugose carbonaceous endocarps in the adjacent Lower Headon Beds. The older *L. cooperi* Chandler from the Oldhaven Beds (Chandler, 1960*a* : 93, pl. 9, figs. 8–10) is larger than *L. forbesi*. Its surface, unlike the marked rugose surface of *L. forbesi* when complete is only slightly rugose.

2. SELSEY, SUSSEX

GYMNOSPERMAE

Order CONIFERALES

Family Abietineae

Genus *PINUS* Linnaeus

Pinus dixoni (Bowerbank) Gardner

1850 *Pinites dixoni* Bowerbank (in part) *in* Dixon, p. 84, pl. 9, fig. 3.
1878 *Pinites dixoni* Bowerbank : Carruthers *in* Dixon, p. 162.
1884 *Pinus dixoni* (Bowerbank) Gardner, p. 66, pl. 13, figs. 1, 2, 5, 8 ; text-fig. 27.
1960 *Pinus dixoni* (Bowerbank) : Chandler, pp. 202, 220, pl. 29, figs. 12, 13 ; pl. 30, figs. 14, 15 ; pl. 33, figs. 75–79.

The original cone from Bracklesham was said by Gardner to be preserved in the Botany Department of the British Museum although in a very imperfect state. It has now decayed. He reproduced Dixon's figure in his text-fig. 27 (1884 : 67). This cone was said to be 5 in. (*ca.* 126 mm.) long by 1½ in. (*ca.* 38 mm.) broad in the upper part. It agreed closely in size with a cone from the Barton Beds (now decayed) figured and described by Chandler (1960 : 220, pl. 33, figs. 75–79). A smaller cone in the Sedgwick Museum (85 by 40 mm.) figured by Gardner (1884, pl. 13, figs. 1, 2) appears to have been almost identical with a beautiful specimen from Hengistbury (75 by 35 mm.) taken by Chandler as the neotype of the species (1960 : 202, pl. 29, figs. 12, 13 ; pl. 30, figs. 14, 15) (V.36352). The exact horizon of these cones is not recorded (see Table, p. 19). Gardner's cone (1884, pl. 13, fig. 8) was decayed when examined by C. Reid.

Pinus bowerbanki (Carruthers) Gardner

(Pl. 9, fig. 50)

1850 *Pinites dixoni* Bowerbank (in part) *in* Dixon, p. 84, pl. 9, fig. 4.
1878 *Pinites bowerbanki* Carruthers *in* Dixon, p. 163.
1884 *Pinus bowerbanki* (Carruthers) Gardner, p. 68, pl. 13, fig. 9 ; text-fig. 28.
1960 *Pinus bowerbanki* (Carruthers) : Chandler, p. 219, pl. 32, figs. 73, 74.

The species was based by Carruthers on very imperfect material and was therefore ill-defined. It appears that the apophyses were not preserved as is obvious from the figure reproduced by Gardner from the original one (1884, text-fig. 28). A second cone (whereabouts not known, probably decayed) was collected by Gardner himself and figured as *P. bowerbanki* (Gardner, 1884, pl. 13, fig. 9). It was about 100 mm. long, 50 mm. broad with apophyses of the scales having a recurved umbo and marked transverse carina. A cone from Barton, imperfect length, 85 mm. ; breadth between 20 and 40 mm., probably belongs to the same species. It was described by Chandler (1960 : 219, pl. 32, figs. 73, 74). Whether these two are really identical with the original mutilated cone cannot now be decided, but since there were two *Pinus* species at Bracklesham, it seems best to retain the name *P. bowerbanki* for these larger cones with sharply carinated apophyses and recurved umbos rather than to introduce another specific name.

A cone (V.3313) purchased from J. J. B. Ogle, 1891, labelled *Pinites Dixoni* Bowerbank, Bracklesham Bay appears to belong to this species. It is imperfect below, 130 mm. long as preserved, with maximum breadth (80 mm. from apex) of about 65 mm. The apophyses are markedly elongate transversely, the largest about 22 by 5 mm.; they are sharply carinate with conspicuous recurved umbo.

Family ARAUCARINEAE

Genus ***ARAUCARITES*** Presl.

Araucarites selseyensis n. sp.

(Pl. 4, figs. 1–5; Pl. 5; Pl. 6)

?1850 *Lycopodites squamatus* Brongn.: Dixon, p. 84, pl. 9, fig. 1.

DIAGNOSIS. Some twigs with broad short spreading leaves, others with narrow acicular leaves. Leaves amphistomatous, the dorsal stomatal bands being restricted in the broader leaves to the lower end and to a small patch or line of stomata (sometimes one stoma only) separated from the main band by a distinct area of ordinary epidermal cells. Sometimes in acicular leaves dorsal stomata absent in the upper half of the leaf, sometimes represented by a narrow line of stomata extending almost to leaf tip. Ventral stomatal bands in all types of leaf extending throughout the length. Many stomata on both surfaces transversely oriented in the broader leaves but some longitudinal or oblique. On the acicular leaves all stomatal bands narrow, the majority of their stomata being longitudinally aligned. Ordinary epidermal cells with numerous small oval pits, commonly rectangular, sometimes slightly narrowed towards their extremities. Cone-scale subquadrangular, broadest at about two-thirds of the length from the base, apex with long parallel-sided process having rounded distal end.

HOLOTYPE. A twig with broad leaves embedded in small clay block (about 45 to 50 mm. in diameter) on back of which is detached cone-scale. Brit. Mus. (N.H.), No. V.41918.

DESCRIPTION. *Twigs:* Varying in habit with broad spreading leaves as in the holotype (Pl. 4, fig. 1) or narrow acicular leaves as in Pl. 5, fig. 7. A twig showing both types of leaves was macerated in order to obtain leaves for cuticle preparation (cf. Pl. 6, fig. 13 and slides V.41920*a–j*). Leaves in all twigs falcate, spirally arranged, sharply pointed, decurrent, normally four-sided, the sides or facets often unequal. Broader leaves often with a wide angle over the midrib on the ventral surface, while some of the lateral leaves may be distorted. In some leaves distortion in growth so great as to produce a bifacial effect. V.41918 is about 25 mm. long with leaves which may measure about 5 mm. from the tip to the point where they spring away from the twig on the dorsal side. V.41919, represented by counterparts, has a more slender appearance and is about 35 mm. long with leaves about 6 or 7 mm. measured as in V.41918 above. The length and narrowness of the leaves on this twig produce much narrower facets but a few broader more spreading leaves were exposed at the base of the twig after the figure in Pl. 5, fig. 7 had been taken. Carbonaceous substance was preserved in all specimens together with impressions in clay but as it was much cracked cuticle preparation was difficult. In particular the dorsal cuticle was cracked and brittle and broke up when mounted permanently after preliminary examination. Yet enough fragments remain to demonstrate some of the outstanding features. All leaves amphistomatous, the stomata being concentrated in well-defined stomatal bands.

Upper surface: Stomatal bands always extend from base to apex but do not merge at the apex in the examples seen. They narrow upwards so that whereas near the base there may be as many as nine longitudinal lines of stomata, near the apex these are reduced to one or two lines per band. Sometimes many stomata in a line are contiguous, eight to ten such having been counted (slides V.41918 *a*, *b*, V.41920*c*). Adjacent lines may also be contiguous but auxiliary cells are never shared either in the same line or in adjacent lines. The stomatal bands are inevitably narrower in the long narrow leaves of V.41919 (cf. also slides V.41919*a*, V.41920*b*). Some of these narrower leaves show only two lines of stomata, or even one, in a band ; others show three or four lines always reduced to one towards the apex. On the decurrent basal flange (V.41918*c*, *e*) there may be two or three lines of oblique stomata above, but one only at the extreme base. In this decurrent region in the broad leaves the cells appear somewhat larger than in the free part of the ventral surface. On the whole in the broad leaves transversely oriented stomata predominate (Pl. 6, figs. 14, 16, 17) although oblique and longitudinally oriented ones also occur. The asymmetry of a leaf may however result in one stomatal band having transverse stomata and the other oblique (slides V.41918*a–c*, *e*, V.41920*c*). Again the band on the broader of two facets in an asymmetrically developed leaf may have more lines of stomata than that on the narrower facet. In the acicular leaves stomata are more frequently longitudinally oriented but transverse and oblique ones may occur. They vary in size, usually being larger on the broader leaves. The outer pore, where measured, ranges from 0·027 to 0·04 mm. There are from four to six auxiliary cells arranged end to end around the pore and these cells are normally differentiated into polar and lateral. There is also commonly a regular outer ring of concentric cells. In the broader leaves the breadth of the auxiliary cells combined with their transparency and the manner in which they sweep around the stomata make the apparati conspicuous as light coloured oval to subcircular patches in the cuticle. Occasionally ordinary epidermal cells are so arranged as to produce three concentric rings in parts of a stomatal apparatus. Where the guard cells abut on the auxiliaries a pair of thick scales is present or there may be a ring of cuticle (Pl. 6, figs. 15, 17). The ordinary epidermal cells of the stomatal bands are often quite irregular in shape and frequently equiaxial. However several transversely elongate and aligned cells commonly occur between adjacent stomata in the same longitudinal row as well as elsewhere sometimes. The three bands of ordinary epidermal cells outside the stomatal bands naturally tend to be wider in the broader than in the acicular leaves, the cells themselves also being broader. In the marginal bands of the broad leaves the two outermost lines of cells are aligned obliquely. In one leaf examined six to ten rows of cells were visible in the marginal bands ; in another there were twenty to twenty-six rows. The median band of ordinary epidermal cells also varies greatly in width, twenty to thirty-eight rows of cells having been counted. These epidermal cells are commonly rectangular in broad leaves and in all leaves are straight-sided not sinuous. They become shorter towards the junction with the twig and may here be equiaxial or even transversely elongate and aligned. In acicular leaves they tend to be relatively narrow and are sometimes narrowed towards their extremities (Pl. 5, fig. 8 ; cf. also slides V.41919*a*, *k*, V.41920*g*). Small oval or subcircular pits irregular in size and distribution are scattered over the cell walls in all leaves (Pl. 6, figs. 15, 19).

Lower surface: The cuticle is somewhat denser with narrower and smaller cells (slides V.41918*f*, V.41920*a*) this character being most marked in acicular leaves (Pl. 5, figs. 9, 10 ; cf. slides V.41919*c*, V.41920*b*, *g*). The stomatal bands, unlike those of the upper surface are almost restricted to the base of the leaf in the broader leaves, sometimes extending for a short distance only onto the free outstanding part (slide V.41918*f*) in other cases occurring only on the decurrent part (slides V.41918*a*, *b*). Hence they always terminate a long way below the corresponding ventral stomatal bands (Pl. 4, fig. 2). Sometimes, however, a few stomata (three were seen in slide V.41918*f* but the tip of this leaf later became disorganized on permanent mounting,) or a short line of stomata are present nearer the apex separated from the main stomatal band by a distinct area of ordinary epidermal cells. In slide V.41918*a* a single isolated stoma occurred in this position (Pl. 4, fig. 2). It is not possible on the amount of material seen to state that these separated patches of stomata are always present, further evidence is needed. In the acicular leaves there may be a long stomata-free tip (Pl. 5, fig. 10) but an asymmetrically developed leaf in slide V.41920*a* (Pl. 5, fig. 9) shows a single line of stomata at the distal end of the leaf surrounded by dense narrow epidermal cells. In this latter case it has not been possible to ascertain whether this line is separated from the main stomatal band below as only the upper half of the leaf was preserved. In the broad leaves seen the stomatal bands may have seven to nine longitudinal lines of stomata at the base the number decreasing upwards. Invariably individual stomata and lines of stomata are more widely spaced than on the upper surface. Frequently two lines have four or six lines of ordinary epidermal cells between them (V.41918*b*, *k*, Pl. 6, figs. 18, 19) which form conspicuous " lanes " in the stomatal band. In these " lanes " the cells are usually rectangular and longitudinally aligned. A few stomata may occur quite close to the margin of a leaf on the narrow decurrent basal region in the middle of ordinary epidermal cells. In the acicular leaves two lines of stomata are common but four to five lines have been seen (V.41919*f*, *i*). Stomata in the broad leaves are oblique or transverse, sometimes longitudinal (V.41918*c*, *d*, *k*) but transverse and longitudinal stomata occur in a single leaf. In the acicular leaves the stomata are commonly oblique or longitudinal and frequently contiguous. As on the ventral surface scales or a ring of cuticle are present at the junction of guard cells and auxiliaries and there is the same stomatal structure but on the whole the stomata tend to be smaller. Pits are conspicuous on the walls of the ordinary epidermal cells in both types of leaf. At least two fragments from a decurrent leaf base showed pits with two concentric rings like bordered pits. In the broad leaves the median band of ordinary epidermal cells displays a variable number of cell rows, eight being seen in one leaf, twenty in another. These cells are most commonly rectangular. In the acicular leaves they are long and narrow with a more noticeable tendency to narrow towards their ends.

A stout twig with acicular curved leaves is figured in Pl. 5, fig. 12. The leaves were angled on both surfaces, the angle on the upper surface being inconspicuous, that on the lower clearly marked as were the lateral angles also. Unfortunately this twig has completely decayed and a mere scrap of cuticle showing the ordinary epidermal cells of the median band was obtained (V.41921). While therefore it probably belonged to the same species as the other twigs this awaits confirmation from further material from horizon Fisher 21 or 22.

It is highly probable, as suggested by Gardner (1883 : 59) that *Lycopodites squamatus* Brongn. (Dixon, 1850, pl. 9, fig. 1) was also an *Araucarites* twig, but as the relationship of the new material either to Brongniart's species or Dixon's specimen cannot be established this specific name has not been adopted.

Female cone-scale (Pl. 4, figs. 3–5) : The detached cone-scale (V.41918) is subquadrangular in outline, broadest at about three-quarters of the length from the base where there are two lateral angles of about 90°. Below this line of greatest breadth the scale is contracted to the basal attachment. Above it the sides converge more rapidly to the apex. At the apex there is an attenuated subparallel-sided process with rounded distal end and slight median ridge on its upper surface. The external apophysis of the scale lies above the line of greatest breadth. It can be seen on the impression to the left in Pl. 4, figs 3, 4 where exposed by the flaking away of the carbonaceous substance. It shows as a marked facet separated by a distinct ridge from the conspicuous longitudinally striate limb of the scale. A less prominent transverse ridge on the upper surface of the carbonaceous scale has flutings, rounded upwards, which are visible on the right in Pl. 4, figs. 4, 5 where the actual substance of the scale is preserved. This substance has cracked on drying along the flutings. Possibly this fluted ridge represents a ligule. Below the ridge (or ligule) the upper surface shows two or three rows of large rounded closely contiguous pits producing a regular pattern for a short distance. Further down the limb there are rectangular cells (larger than those in an *Araucarites* scale from the Upper Headon of Colwell awaiting description). They give rise to longitudinal striations coarser than the ones in a corresponding position on the lower surface of the scale. In addition there are more conspicuous longitudinal rounded ridges and grooves giving rise to flutings due to thick resin ducts in the wall of the scale. The ducts lie opposite to and alternating with the apices of the rounded flutings of the ridge and are from 0·2 to 0·4 mm. apart. On drying the resin swelled, rupturing the thin tissues which originally covered the ducts so that solidified resin was thereby exposed. Two small matrix-filled apertures are seen on the upper surface just below the base of the terminal process (Pl. 4, fig. 5) which appear to lead into canals. A longitudinal section at right angles to the breadth exposed by the rupture, through drying, of the carbonaceous scale revealed a small cavity indicated superficially by a slight median convexity. It extended only for a short distance down the scale. A second smaller cavity with a transversely striate lining layer lay behind it in the thickness of the scale. The significance of these cavities is not clear. No seed seen. Length of scale including apical process, 16 mm.; maximum breadth, 11 mm.; length from tip of spine to line of greatest breadth, 7 mm.; length of limb below line of greatest breadth, 9 mm.; length of spine, 4 mm.

Remarks and affinities. The association of female cone-scales similar to the one described above with foliage of *Araucarites* type at Bembridge (Pl. 4, fig. 6), Selsey and Célas (Alais basin, France) points to a connexion between scales and foliage confirmed by actual organic continuity in the Célas material described by Marion as *Doliostrobus* (1888 : 1–20, pls. 1, 2). The scale from Bracklesham Bay has therefore been referred with the associated foliage to *Araucarites selseyensis*. Despite differences of habit shown by the foliage the cuticle structure appears to indicate that the twigs belong to a single species. This is distinguished in the best preserved broad leaves from the more or less contemporary *Araucarites* in the Bournemouth Beds by the restriction of the stomata on the dorsal surface to a stomatal band at the base of the leaf with sometimes a small area, separated from the main band, nearer the leaf tip as described above. In the Bournemouth species the dorsal stomatal bands extend throughout the length of the leaf ending only a short distance below those of the ventral surface. *A. selseyensis* is also distinguished by the more regular rectangular ordinary epidermal cells particularly in the broader leaves, with their clearly defined irregularly scattered pits. Also a larger proportion of the stomata are transversely oriented. A fragment of cuticle from Bournemouth has been described by Bandulska (1923 : 248, pl. 20, figs. 13, 14) and more awaits publication in a monograph of the Bournemouth Flora.

The distribution of the dorsal stomata also distinguishes *A. selseyensis* from *A. gurnardi* Florin from the Bembridge Beds, Isle of Wight (*in* Reid & Chandler, 1926 : 48) where again the dorsal stomatal bands extend almost throughout the length of the leaf. However the ordinary epidermal cells of *A. gurnardi* more nearly resemble those of *A. selseyensis* in being rectangular-ended and conspicuously pitted.

An Australian species of probable Oligocene age described by Cookson & Duigan (1951 : 428, pl. 3, figs. 19–24) and actually referred to the genus *Araucaria* itself as *A. lignitica* shows a somewhat similar distribution of stomata which the authors point out is found in seven living species of *Araucaria* of the section Eutacta. In this case the characters of the female cone, seed and male cones confirm the relationship.

As regards the scale of *A. selseyensis* it appears quite distinct from the Bembridge scales (Pl. 4, fig. 6, also Reid & Chandler, 1926 : 52, pl. 2, figs. 17, 18) and from a Colwell Upper Headon scale mentioned above on account of its narrower, more attenuated form, possibly also on account of the long apical process which may however be incomplete in the Bembridge and Colwell material. The cone-scales of the Bournemouth *Araucarites* are not known. There is a close resemblance between the scale of *A. selseyensis* and those of Marion's *Doliostrobus Sternbergii*. Both have a similar cuneate form with steep-sided apex and long apical process. *Doliostrobus* is known to show great variation in scale size in accordance with the position in the cone e.g. one scale was 17 mm. long, 12 mm. broad and the distance from the tip of the spine to the line of maximum breadth was 10 mm. The largest scale depicted was about 18–20 mm. long (including the spine), the smallest 8 mm. A consistent difference lies in the sharply pointed tip of the spine of *Doliostrobus* as against the rounded tip of *A. selseyensis*. No leaf cuticle structure is known in the case of *Doliostrobus*.

The cuticle, form of foliage, and scale with long process in the Selsey material indicate Araucarian affinities, but more information is needed as regards the cone-scales and seed structure before it can be referred to the living genus *Araucaria*. Hence the reference to the conventional genus *Araucarites* as *A. selseyensis*.

ANGIOSPERMAE

Class MONOCOTYLEDONES

Family POTAMOGETONACEAE

Genus ***LIMNOCARPUS*** C. Reid emend. Reid & Chandler, 1926 : 68

Limnocarpus forbesi (Heer)

(Pl. 7, figs. 22–24)

1862 *Cyperites Forbesii* Heer, p. 373, pl. 18, figs. 20, 21.
1888 *Cyperites forbesii* Heer : Gardner, p. 422, pl. 3, fig. 16.
1888 *Carpolithes headonensis* Gardner, pp. 420, 423, pl. 3, fig. 30.
1898 *Limnocarpus headonensis* (Gardner) C. Reid, p. 464, text-fig. p. 465.
1925 *Limnocarpus headonensis* (Gardner) : Chandler, p. 13, pl. 1, figs. 4*a–c*, text-fig. 3.
1926 *Limnocarpus headonensis* (Gardner) : Reid & Chandler, p. 70, pl. 4, figs. 1–3.
1960 *Limnocarpus headonensis* (Gardner) : Chandler, pp. 205, 222, pl. 30, figs. 16, 17 ; pl. 33 figs. 84–86.

DESCRIPTION. *Endocarp:* Subovoid with large deep pit on each broad surface at about one-third of the length of the endocarp from the apex (Pl. 7, figs. 22, 24). Style long, patent, slightly reflexed at apex when perfect (Pl. 7, fig. 23), terminal on the ventral margin. Short stalk persistent. Germination valve narrow-ovate arising near the stalk but not reaching the style base, with three strong longitudinal ridges one median and two marginal. Lateral ridges only slightly tubercled. Broad surfaces rugose and pitted, the pits formed by the merging of adjacent rugosities. Length of endocarp, 1·75 mm. including style (about 0·25 mm.) ; breadth, 1·25–1·3 mm. ; thickness, about 1 mm. A smaller abraded endocarp measured : length, 1·5 mm. ; breadth, 1 mm. ; thickness, 0·75 mm.

REMARKS. The species is represented by three figured and five unfigured (V.41873) specimens. They agree with the species hitherto referred to *L. headonensis* (Gardner). It occurs in the Lower Headon of Hordle and the Bembridge Beds as well as in the Hengistbury and Barton Beds. There are unpublished records in the Lower and Upper Headon of Colwell Bay, Isle of Wight and in the Bournemouth Marine Beds. The occurrence of the endocarps in enormous quantities in estuarine beds e.g. in the *Limnocarpus* Band at Hordle, indicates a gregarious habit probably in brackish lagoons or quiet backwaters. Reid & Chandler (1926 : 71) expressed the opinion that fruits named *Cyperites forbesi* by Heer (1862 : 373, pl. 18, figs. 20, 21) were probably crushed specimens of *L. headonensis* (as it was then named) but as no extant material of *C. forbesi* was known and Heer's figures and description were inadequate the suggestion could not be confirmed. Recently a hand specimen (No. 6712) labelled *Cyperites forbesi* Heer full of crushed *Limnocarpus* has been seen in the Geological Survey Museum where Heer's specimens from Hamstead are preserved. It is believed to be Heer's figured specimen (1862, pl. 18, figs. 20, 21) and is so labelled with a query. Other fruits (No. 76921) similarly labelled *C. forbesi* (Burdett Coutts collection) confirm this relationship. Hence under the rules of nomenclature *Limnocarpus headonensis* must now be referred to *L. forbesi* (Heer) since the genus *Cyperites* was first created by Lindley & Hutton for Cyperaceae leaves and was subsequently used by Heer for *all* remains of Cyperaceae of unknown generic affinity. *Limnocarpus* is definitely referred to Potamogetonaceae and is therefore retained as the generic name of this species.

Limnocarpus? enormis n. sp.

(Pl. 7, figs. 25–33)

DIAGNOSIS. Endocarp ovoid with large scattered tubercles. Style long straight, ventral margin with conspicuous rounded ridge. Internal condyle short associated with a small inconspicuous comma-shaped depression on each side of the ventral edge at about one-third of the length from the apex. Keel with three longitudinal tubercled ridges having also a few scattered tubercles on the surface between the ridges. Size very variable. Length (including style) about 2·5–3·5 mm.; breadth, 1·75–2·5 mm.; thickness, 1·5–2 mm.

HOLOTYPE. V.41874.

DESCRIPTION. *Endocarp:* Ovoid (frequently somewhat flattened in fossilization) with long patent style more or less terminal on the ventral margin and slightly forwardly directed. Ventral margin with a conspicuous longitudinal rounded ridge. Broad surfaces with large scattered rounded tubercles conspicuous in unworn specimens (Pl. 7, figs. 25, 30) but scarcely seen in worn ones (Pl. 7, figs. 26, 28). Keel (germination valve) ovate, broad, arising near the basal attachment but not extending to the base of the style having three conspicuous longitudinal ridges, one median and two marginal bearing a few low rounded tubercles. A few scattered tubercles also lie between the ridges (Pl. 7, figs. 27, 32, 33). Lateral pits differing from those of *Limnocarpus forbesi* in being very inconspicuous, long and narrow, comma-shaped close to the ventral ridge arising not far below the style base and directed towards the ridge narrowing downwards. Sometimes they are indicated only by a line of close-set tubercles externally (Pl. 7, figs. 29, 30). Internally these pits are associated with only a small process on the locule wall (Pl. 7, fig. 31). External surface of obscure equiaxial cells. Seed not preserved but from the character of the locule it can have been only slightly emarginate near the hilum around the small process and with a large lower and small upper limb. Locule lining of small equiaxial cells with large cavities. Dimensions very variable. The following are examples: 1) Length (including 1 mm. long style), 3·5 mm.; breadth, 2 mm.; thickness, 2 mm. Valve or keel missing extending to 0·3 mm. from style base. 2) Length (including style, 1 mm.), 3·25 mm.; breadth, ·2 mm.; thickness, 1·5 mm. Keel missing, endocarp collapsed below. Lateral pits begin at approximately 0·5 mm. from style base and extend for about 1 mm. (Pl. 7, fig. 26). 3) Length (including style, 0·5 mm.), 2·5 mm.; breadth, 1·75 mm.; thickness, 1·6 mm. Keel preserved. 4) Length (style missing), 2·5 mm.; breadth, 1·75 mm.; thickness, 1·75 mm. Keel missing. 5) Detached keels *ca.* 2–2·5 mm. long, 1·2 mm. broad. 6) Length of style in broken endocarp, 1 mm. Length of endocarp incomplete. Breadth, 2·5 mm. Foramen indicated by flanking tubercles (Pl. 7, fig. 30).

Remarks. Represented by seven endocarps (some imperfect), two detached keels and three fragments. They appear to differ from the genus *Potamogeton* and from *Limnocarpus forbesi* in the less curved seed-cavity and from *Ruppia* in the gently curved ventral margin which is unlike the gibbous margin of that genus and in the keel arising near the peduncle. Although the resemblance is greatest to *Limnocarpus* the fruits are referred to it only doubtfully as there may be other genera as yet unknown to the writer which are more comparable. From all the fossil species of Potamogetonaceae previously described it is distinguished by its large size and the closeness of the comma-shaped inconspicuous lateral pits to the ventral margin. There is no evidence as to whether the low tubercles scattered over the surface were originally spines.

Genus?

(Pl. 8, fig. 38)

Description. *Rhizome:* Repeatedly branched with close-set nodes and long narrow transversely elongate and oriented leaf-scars which do not completely encircle the stem but appear to embrace about half its circumference. One leaf-scar underlies each node but it is not clear whether there are additional scars between the nodes. The scars show traces of several bundle fibres. The branches arise in the axils of the leaves. One branch *a* (Pl. 8, fig. 38) is seen on the right at the base (as preserved) and extends for about 28 mm. before it is broken at the edge of the stone. At its point of origin it is very small but it broadens rapidly upwards to 6 mm. in diameter. Its exposed upper surface shows at least six leaf-scars and the cut transverse end of another branch on the right at *b* (Pl. 8, fig. 38) close to its origin. The main stem is visible for a short distance only as it is broken above the second node. It bears another branch *c* (Pl. 8, fig. 38) on the left in the axil of a conspicuous leaf-scar. About 6 mm. of this branch is preserved before it reaches the edge of the stone where it is about 5 mm. broad. A small circular funnel at one node may indicate the point of emergence of another branch now broken. No roots have been seen but these, if present would lie on the lower surface of the rhizome and be concealed by matrix. The leaf scars project, each internode gradually increasing in diameter upwards so that the rhizome has a distinctive jointed appearance. Surface covered by a thick shining somewhat dimpled epidermis which is formed of small square or rectangular cells about 0·008–0·009 mm. in diameter. The slightly thickened lateral walls of these cells give a fine longitudinally striate appearance and on drying the epidermis and rhizome tend to crack along the striae. Inside the stem there are traces of large air-cells or cavities varying much in size, the largest being about 0·027 mm. in diameter. Subglobular pyrites casts sometimes occupy their cavities and are conspicuous when the carbonaceous walls have decayed.

Leaf : A detached parallel-sided fragment of an elongate leaf *l* (Pl. 8, fig. 38) lies athwart the lower end of the specimen but almost certainly belongs to it as indicated by its identical epidermal structure. The tip (seen on left) is blunt and rounded. The width is 2 mm. but only about 13 mm. of the length are preserved. There are traces of several parallel longitudinal nerves.

REMARKS. This unique specimen, found by Curry in Fisher Bed 21 at Selsey, suggests at a first glance rhizomes radiating from a centre although closer examination shows repeated branching at successive levels. The jointed stem with large leaf-scars is highly characteristic of certain marine genera of Potamogetonaceae such as *Posidonia* and *Cymadocea*. Gardner (1886 : 400) reported that the surface of one of the Bracklesham Beds was " dotted over " with " *Posidonia* " but added that " the rhizomes radiate from a centre, whilst in the French and other European fossil species they are long and branching ". It appears highly probable that V.41922 is a rhizome of the supposed " *Posidonia* ". The living *Posidonia* has close-set leaf-scars and a jointed rhizome thickly clothed with shredded remains of leaves reduced to bast fibres. *Cymadocea* shows similar features. The generic relationship cannot be regarded as finally established and the possibility that these rhizomes may belong to one of the species of the extinct *Limnocarpus* found in the Bracklesham Beds of this area cannot be excluded. It does at least seem clear that it represents a genus of Potamogetonaceae with jointed rhizomes. Whether there is a connexion with the branches and buds of Genus? (see Pl. 7, figs. 35–37 ; Pl. 8, figs. 39–48) is again purely a matter for speculation on evidence at present available.

Family POTAMOGETONACEAE?

Genus?

(Pl. 7, figs. 35–37 ; Pl. 8, figs. 39–48)

DESCRIPTION. Buds or bulbils preserved in two different ways giving different appearances. Some, seen from the side, are oval or oboval in outline, originally ovoid but compressed in fossilization, truncated at the base by a large slightly sunk attachment scar now ellipsoidal originally subcircular. From the edges of the scar can be traced overlapping three or four stiff rather pointed bud-scales or bracts with irregularly toothed upper margins. The scales are represented by casts of their inner surfaces with traces only of organic substance. They are seen in V.41895–96, V.41902, V.41907, V.41909 (cf. Pl. 8, figs. 43, 45). Others, the most numerous, are usually larger and inflated, subglobular and they show very clearly the basal sunk circular attachment scar with punctations marking points of entry of a number of fibro-vascular bundles. These clearly represent internal casts of the external scales, the growing point and inner scales having presumably decayed, their place being taken by a mud-cast of the globular cavity thus formed. Such mud-casts are preserved in V 41889–94, V.41900 (cf. Pl. 7, figs. 35–37, Pl. 8, figs. 39–45). In V.41890 (Pl. 7, fig. 36) and V.41897, scales still remain adhering to the mud, the former specimen also showing the internal mud-casts last described still adhering to the scales. In V.41902 near the basal scar thin-walled areoles, about 0·038 mm. in diameter are visible in small patches, each areole being occupied by minute equiaxial convex rounded cells, also seen in V.41895. These cell patches represent organic tissues still adhering to the casts or their impressions. Obscure longitudinal striation is seen in V.41894 and V.41895 suggesting veins although no actual fibres are preserved. Certain of the buds show an asymmetric development as in V.41891 and V.41897 (Pl. 7, fig. 37 ; Pl. 8, fig. 46) probably indicating that they have begun to grow out laterally. A further stage of growth is seen in V.41899 (Pl. 8, fig. 48). Buds arise at the nodes of a puckered or flanged stem fragment (V.41890, Pl. 7, fig. 36) but sometimes from a flatter more ribbon-like stem (V.41892 ; and Pl. 8, fig. 39). They may be solitary and alternate or several may be associated at one level. The stems retain remains of carbonaceous tissues and show the impressions of thin-walled cells about 0·038 mm. in diameter like those on the bracts (V.41889, V.41892). There is also obscure evidence of flat ribbon-like finely longitudinally striate leaves always very imperfect. One arises from a node in V.41889 (cf. Pl. 7, fig. 35). Occasionally when the globular internal casts are broken from the stems a deep cup-like hollow is exposed with circular cavity at its base. It is surrounded by puckered remains of scales (V.41901). In V.41889 basal scales are well seen with the bud-cast in profile projecting from between them. This cast also has fine concentric puckerings on its surface suggesting that the surrounding bracts (now gone) had a diaphanous thin lining. Dimensions vary considerably according to the stage of development. Examples of the subglobular casts are : 1) Length, 3 mm. ; breadth, 2·5 mm. 2) Length, 2·75 mm. ; breadth, 3·25 mm. 3) Length, 1·6 mm. ; breadth, 1·7 mm. 4) Length, 1·6 mm. ; breadth, 2·16 mm. Diameter of basal scar, 1·25–2 mm. Transverse diameter of dorsiventral flattened detached casts, 2·5 by 2·5 mm. ; 2·4 by 2·4 mm. Examples of the laterally flattened ovoid buds are : 1) Length, 2·16 mm. ; breadth, 1·1 mm. 2) Length, 3·2 mm. ; breadth, 2 mm. 3) Length, 3 mm. ; breadth, 2 mm.

REMARKS AND AFFINITIES. Twenty-nine specimens (V.41889–V.41917) show obscure fragments of stem and leaf with buds (or bulbils) connected with propagation or the formation of lateral branches. All were derived from the small rolled clay pebble which yielded an *Araucarites* twig with cuticle (see p. 19). The evidence for a water plant lies in the character of the large thin-walled areoles or cells. The possible indications of parallel longitudinal nerves suggest Monocotyledones. The buds with circular attachment scar could belong to Cyperaceae, Gramineae or Potamogetonaceae, but scales with denticulate margins appear to exclude relationship with the two first-named families so far as these could be examined. The specimen is referred tentatively to Potamogetonaceae but the genus cannot at present be determined. There is as yet no evidence to connect these fragments with *Limnocarpus* which also occurs in the Bracklesham Beds of the Selsey area.

Family CYPERACEAE

Genus ***SCIRPUS*** (Linnaeus)

Scirpus lakensis Chandler

1960 *Scirpus lakensis* Chandler, p. 206, pl. 30, fig. 26.

The apical end of a characteristic fruit showing the contraction at the style. Only the inner yellow shining translucent integument is preserved but it shows clearly the characteristic longitudinal ridges and transversely elongate hexagonal cells.

Genus ***CARICOIDEA*** Chandler, 1957 : 86

Caricoidea obscura Chandler

(Pl. 7, fig. 34)

1960 *Caricoidea obscura* Chandler, pp. 207, 223, pl. 30, figs. 27–33, 34? ; pl. 33, figs. 98–105.

DESCRIPTION. A typical fruit, subovoid in outline, truncated below by a large foramen which marks the attachment, rounded at the stylar end. The surface is much abraded but shows the corky wall formed of small equiaxial cells. Length of fruit, 1·75 mm. ; breadth, 1·25 mm. ; breadth of (flattened) basal truncation, 0·5 mm.

REMARKS. The holotype of this species is from Cliff End, near Mudeford. The species also occurs in the Lower Bagshot and Bournemouth Freshwater and Marine Beds.

Family NIPACEAE

Genus ***NIPA*** Thunberg

Nipa burtini (Brongniart)

(Pl. 9, fig. 49 ; Pl. 10, figs. 51–53)

1894 *Nipadites Burtini* (Brongniart) : Rendle, pp. 147–150, pl. 6.
1897 *Nipadites Burtini* (Brongniart) : C. Reid, pp. 6, 7, fig. 11.
1960*a* *Nipa burtini* (Brongniart) : Chandler, p. 133, pl. 14, figs. 4–9.

Undoubted large drifted fruits of *Nipa burtini* " about the size of a coconut " were obtained by Clement Reid from Cakeham Beds A and many had been seen earlier by Gardner. One specimen figured by Reid (1897, fig. 11) had previously been figured by Rendle, natural size (1894, pl. 6). When efforts were made to preserve it, it began to break up but remains showing the grey quartzose matrix were formerly in the British Museum (Natural History). As in the case of the Boscombe *Nipa* fruits the preservation made it difficult to keep them for long. The carbonized sand-filled hulls were liable to crumble on being taken from the damp beach while the carbon films cracked and peeled, hence it may be assumed that such specimens would not drift intact far from the beds in which they lay. The published figures show a longitudinally angled fruit, incomplete at the base, umbonate at the apex, typical of *N. burtini*, and about 13 cm. long, 11 cm. broad. An undated letter from Gardner to Clement Reid states " the Bracklesham fruits [Nipas] are always the same size and nearly as large as the Belgian ones ". Gardner added that it was years since he had found one at Bracklesham and he thought that the beds had since been covered up. Curry records (1958 : 15) that the Cakeham Sandstone with fruits of *Nipa* has not recently been seen.

Two smaller very differently preserved pyritized *Nipa* fruits found loose on the shore by S. Garner are figured (Pl. 10, figs. 51, 52). They show marked differences in size and development and resemble the Sheppey specimens in their preservation. Mr. Curry (*ex. lit.*) reports that they are probably from the Palate Bed (Fisher 4) which has fairly frequently been exposed in recent years, he himself having found similar pyritized fruits *in situ* at this horizon as well as loose on the shore (V.32593) in the neighbourhood of this bed. V.29214 is a small flattened oboval immature fruit, slightly imperfect at the extreme base. Its surface is longitudinally angled and smooth and evidently represents the epicarp. Obscure, ill-preserved, oblong, longitudinally aligned cells are seen. Length of fruit (as preserved), 5·8 cm. ; maximum diameter, 3·6 cm. ; diameter at right angles to this, 1·5 cm. V.40260 is a fragment, 6·7 cm. long, 5 cm. broad, of a much better developed fruit showing part of the fibrous sarcocarp ; when complete this fruit must have been at least 10 cm. long and 6 cm. broad but the breadth is imperfect and the apex much broken. The outer layers are worn so that at the lower end part of the margin of the foramen for germination is visible. Impressions of the stout longitudinal fibres of the sarcocarp are seen all over the surface but the parenchyma cells between them are obscure. There are no details of seed structure on the ill-preserved concave inner side of this fragment but its form and the size of the concavity on the reverse side suggest that it once contained a well-developed seed. A third fruit incomplete at base and apex, 38 mm. broad was found by L. Garner (V. 29215) in the same sort of position.

Reid (1897 : 6) describes the finding of a single *Nipa* close to the *Turritella* Beds and to the channel that runs from Earnley (i.e. near the outcrop of the Palate Bed). Although this fruit is no longer extant and its mode of preservation is not described the locality suggests derivation from the Palate Bed especially as the carbonaceous sand-filled shells from Cakeham would be unlikely to survive transport for such a distance.

One extremely small immature much ribbed fruit (V.33732) is almost certainly of Lutetian age (communication from Mr. Curry) as the loose block of matrix in which it was found is full of *Nummulites laevigatus* which only occurs abundantly in Fisher Bed 6, a bed of which only small areas have been seen while its lower part is decalcified and weathered and buried under Pleistocene and Holocene mud. The lower end of the small fruit is buried in the matrix, the length must have been about 10 mm. ; maximum breadth, 4·5 mm. The surface at the upper exposed end shows a film-like layer of rounded equiaxial cells about 0·028–0·038 mm. in diameter exactly comparable with cells seen at the upper end of living *Nipa* both in mature and immature specimens. Lower down the fruit, Recent and fossil, the superficial cells become somewhat elongate and longitudinally aligned giving rise to longitudinal striations.

A collection of at least seven very perishable fruits (V.35743) was made by Mr. Curry in an area of about 50 square yards on the surface of the Eocene clay eastwards of Bracklesham. The condition of the specimens was such that they could not have travelled far and Mr. Curry considered that they were probably from Fisher Bed 7 or 8 and must certainly in any case be Lutetian. The largest specimen (V.35722) is shown in Pl. 9, fig. 49 ; it was about 19 or 20 cm. long and about 11 cm. broad. Another long narrow fruit, slightly imperfect at the apex, was about 15 by 6 cm. Other specimens were mere fragments of the broadest part of the fruits they represented.

A noticeable feature of this batch of specimens is that one side only is preserved ; on the reverse side is matrix with, or without, embedded fragments of fruit. Some specimens are overlain by an incrustation of pyritized sand which may mask them almost completely. The matrix in all cases is a somewhat glauconitic quartz sand bound by ferruginous cement and the whole specimen is brittle. The carbonaceous substance of the fruits shows, when fresh, the striate surface and long narrow cells of the smooth epicarp in the middle and lower regions, and underneath this are the coarse fibres (conspicuous) and parenchyma (obscure and much pyritized) of the sarcocarp. These tissues are compressed and have become very thin. They quickly disintegrate by cracking into rectangular fragments.

Class DICOTYLEDONES

Family LAURACEAE

Genus ***LAUROCALYX*** Reid & Chandler, 1933 : 219

Laurocalyx sp.

(Pl. 10, figs. 54, 55)

DESCRIPTION. *Cupule* (V.41885) : Broadly obconical (now somewhat flattened in fossilization), rather abruptly narrowed into the thick peduncle, smooth rimmed without sepals. Thick walled. Surface wrinkled and puckered, conspicuous longitudinal wrinkles occur in the lower half and are continued on to the stalk, while equally marked transverse wrinkles are seen at the rim of the cupule and parallel with its margin. Fine irregular convex more or less equiaxial puckerings of varying shape are found all over the surface. Surface cells very obscure, but apparently originally convex and equiaxial, about 0·013–0·018 mm. in diameter. These cells are now almost obliterated by the stresses due to crushing which may have produced narrow parallel bands variously oriented and having close parallel striae at right angles to the length. Some of the rounded convexities of the surface suggest the presence beneath them of secreting glands. No berry was preserved but the scar of attachment of the fallen berry is seen in the base as a dull unpolished area, presumably it was originally circular, now, through compression, 10 by 4 mm. in diameter. Length of cupule including stalk, 18 mm.; transverse diameter as crushed, 20 by 6 mm. (probably originally about 15 or 16 by the same).

REMARKS AND AFFINITIES. It is impossible to tell the generic relationship of this empty cupule but clearly it belongs to the family Lauraceae. It is most probably derived from the Lutetian horizon (Fisher Bed 7) near to which Mr. Curry found it.

Family EUPHORBIACEAE?

Genus ***WETHERELLIA*** Bowerbank emend. Reid & Chandler, 1933 : 251

Wetherellia dixoni (Carruthers)

(Pl. 10, figs. 56–63; Pl. 11, figs. 64, 65)

1850 *Cucumites variabilis* Dixon (non Bowerbank), p. 84, pl. 9, fig. 2.
1850 " Undetermined fossils " Dixon, pl. 12, fig. 20.
1878 *Carpolithes Dixoni* Carruthers *in* Dixon, p. 164, pl. 9, fig. 2; pl. 12, fig. 20.
1954 *Wetherellia dixoni* (Carruthers) Chandler, p. 173.

EMENDED DIAGNOSIS. Fruit a loculicidal and septicidal syncarpous capsule, originally subglobular but somewhat dorsiventrally depressed, beset externally with hollow spines. Carpels so far seen four to at least eight, locules and septa marked by longitudinal external ribs or angles. Seeds usually shorter in proportion to their breadth than those of *W. variabilis* Bowerbank. Length of fruit (frequently distorted), 4–16 mm.; breadth, 13–20 mm. Seeds (much distorted), length, 3·7–7 mm.; breadth, 1·4–4·75 mm.; thickness, 1–1·5 mm.

HOLOTYPE. A five-carpelled syncarpous subglobular capsule falling into segments along loculicidal and septicidal planes of dehiscence. Surface showing spine-bases. Seeds shorter in proportion to the breadth than in *W. variabilis*. Brit. Mus. (N.H.), No. 40509.

DESCRIPTION. Originally spiny with spine-bases or internal casts of hollow spines alone remaining (V.29218, V.29220, V.33827 and 40509). Syncarpous with from four to at least eight radially arranged carpels (possibly more). Carpels often unequally developed at the opposite ends of a transverse diameter giving the fruits a lop-sided arrangement (Pl. 11, fig. 64). Subglobular but usually somewhat dorsiventrally compressed, the compression much increased by fossilization, occasionally laterally compressed (40259). Longitudinal ribs or angles correspond with the locules and septa, so that there are at least eight to sixteen longitudinal ribs. Dehiscence both septicidal and loculicidal (Pl. 10, figs. 56, 58). Axis fibrous giving off coarse branching fibres which pass more or less transversely across the septal walls of the cocci to the exterior of the fruit. These fibres, and others in the thickness of the pericarp apparently terminated in external spines (Pl. 10, figs. 57, 59) which were hollow as indicated by thin shining pyrites internal casts (V.33827) and especially abundant in the furrows between the ribs and angles. Locules extending almost from base to apex of the fruit, and from the axis almost to the periphery, so much compressed tangentially as to be flat except for a narrow inflated area occupied by the seed. The seeds are solitary in the locules, pendulous, suspended by long arched funicles (about 2 mm. in length) from a point on the axis about one-sixth to two-sevenths of the length of the fruit from the apex. They lie somewhat obliquely in the locules so that the distal end is nearer to the axis than the proximal end. Locule lining formed of cells, 0·01 mm. in diameter, aligned so as to produce a general appearance of radial striation. The walls between the locules are thick, formed of coarse equiaxial angular cells, but the structure is often obscured by carbonization which causes the fractured surfaces to appear vitreous and structureless. Dimensions of several fruits, all more or less dorsiventrally compressed or otherwise distorted: 1) Length (holotype), 7 mm. along axis; diameter, 13·5 mm. 2) (V.33825) Length, 4 mm.; diameter, 15 mm. Dimensions of some laterally crushed fruits which therefore show maximum length (V.40259): 1) Length, 16 mm.; diameter, 20 mm. 2) Length, 11 mm.; diameter, 17 mm. 3) Length, 14 mm.; diameter, 14 mm. Some small abortive fruits (V.40259) with minute flat immature seeds measured about 10–12 mm. in both length and diameter. See also V.33827 and V.41923 with abortive seeds.

Seed: Oval or elongate-oval, anatropous, narrowed towards the hilum, chalaza at the broader extremity. Testa thin, formed of a single layer of equiaxial polygonal or quadrangular cells, 0·025 mm. in diameter. Dimensions of much distorted seeds: 1) Length, 4·7 mm.; breadth, 1·4 mm. 2) Length, 3·3 mm.; breadth, 3·3 mm. 3) Length, 5·5 mm.; breadth, 4 mm.; thickness, 1 mm. 4) Length, 7 mm.; breadth, 4·75 mm.; thickness, 1·5 mm.

Remarks and affinities. The most abundant plant fossil of the Selsey shore represented in the British Museum (Natural History) alone by well over a hundred specimens. The horizon or horizons from which these fruits are derived is unknown except in the case of V.41923 from Bracklesham Beds, foreshore at Bracklesham at low-tide mark about twenty yards east of Bracklesham Lane end (probably equivalent to the top of Fisher Bed V at Whitecliff Bay—Cuisian?). They are carbonaceous and unlike *W. variabilis* relatively thin-walled and very light in weight and therefore capable of being drifted along the shore by tides and currents.

The generic position of these fruits is clear. The genus *Wetherellia* was placed tentatively in the family Euphorbiaceae for reasons given by Chandler (1954: 175). The Bracklesham fruits appear to belong to a distinctive species, for up to the present there is no evidence of external spines in *W. variabilis*, the locules of which vary in number from two to five (four to eight at least in *W. dixoni*), the walls appear thicker and its fruits are therefore less liable to distortion, the external angles and ribs are less marked, the seeds relatively longer in proportion to their breadth, while the dehiscence is commonly septicidal first and later loculicidal.

Wetherellia sp. (***? W. dixoni***)

(Pl. 11, figs. 66–68)

Description. *Fruit:* Originally two-loculed, ellipsoid or subovoid but now represented by a single one-loculed semiellipsoid coccus which has resulted from the septicidal splitting of the fruit. Ventral surface flat, dorsal rounded. A median longitudinal suture on both faces indicates the plane of the locule but loculicidal dehiscence has been prevented by the infiltration of mineral cement. Remains of the axial fibres are seen along the suture line on the septicidal inner surface. From the axis one distinct fibre is given off on its right side which is directed radially for a short distance, it then forks, the lower fork quickly disappearing into the thickness of the wall, the other curving upwards and giving off subsidiary branches which also penetrate the wall. Carpel thick and woody with indications of coarse equiaxial parenchymatous cells. Locule lining close-textured seen in section but its surface cells not visible. External surface of coccus slightly rugose owing to a few scattered spine or hair-bases forming short protuberances with a central hollow now filled with matrix or calcite. Length of coccus (slightly broken at apex), 21 mm. Estimated complete length about 30 mm.; breadth, 24 mm.; thickness in plane of locule, 10 mm. Seed not seen.

REMARKS. The specimen is a mineral impregnated carbonaceous coccus together with its concave external mould preserved in a coarse-grained grey sandstone block full of lignite fragments from Cakeham Beds A. Owing to the coarseness of the matrix and the mineralization of the specimen fine details of structure are somewhat obscure, but there is indubitable evidence of hair-bases both on the coccus and its cast. The large size of the specimen is a striking feature. The coccus fits the cast exactly so that no shrinking has occurred probably owing to infiltration of mineral matter into the carbonaceous substance. The complete length of about 30 mm. is in excess of a rare maximum of 26 mm. in *Wetherellia variabilis* Bowerbank (20 mm. is the published maximum) and 16 (allowing for distortion) or possibly 20 mm. in *W. dixoni*. It is necessary in making comparison to remember that *W. variabilis* from the London Clay is always much pyritized, the cells being distended by infiltration of pyrites, hence the measurements given represent the maximum known for that species. On the other hand *W. dixoni*, is carbonaceous, relatively unpyritized and usually much crushed and may easily have shrunk to half or one-third of its original dimensions. On these grounds the Cakeham fossil more resembles *W. dixoni* than *W. variabilis*. The poorly preserved evidence of external spines also recalls *W. dixoni*. Against this relationship are two facts, first, that the specimen was clearly two-loculed when perfect and this character is seen in specimens of *W. variabilis* but not as yet in *W. dixoni*; second, that as in *W. variabilis* the conspicuous or primary splitting has been septicidal, whereas in *W. dixoni* it is frequently loculicidal. It is possible to account for this latter fact by early infiltration of calcite into a primary incipient loculicidal fissure which on crystallizing acted as a cement or in the case of *W. variabilis* from the London Clay by infiltration of pyrites, but if so it is curious that the cementing should have occurred in the loculicidal planes rather than between the closely adpressed septicidal surfaces. While awaiting fresh evidence it seems advisable to refer the specimen to *Wetherellia* sp. (*W. dixoni*?) bearing in mind the possibility that a distinct species may be represented, or that *W. variabilis* and *W. dixoni* will prove to be inseparable given a sufficiently large range of material showing varying types of preservation.

? ***Wetherellia variabilis*** Bowerbank

(Pl. 11, fig. 69)

1840 *Wetherellia variabilis* Bowerbank (pars), p. 84, pl. 12, figs. 1–5, 8–40.
1933 *Wetherellia variabilis* Bowerbank : Reid & Chandler, p. 251, pl. 9, figs. 7–22.

A small coccus, flattened on the inner septicidal surface, angled on the outer face, along the plane of loculicidal splitting, and elliptical in outline was washed by Mr. Curry from the *Turritella* Bed (see Table, p. 18). Loculicidal splitting has started. Typical coarse angular parenchyma is seen in the thickness of the wall. Length, 16 mm. ; breadth, 6 mm. ; dorsiventral thickness, 4 mm.

The specimen from the Lower Lutetian had collapsed on drying but was repaired by Mr. Curry.

The flat ventral surface of the coccus suggests a two-carpelled fruit. The walls appear thick and there are no traces of external spines, but the specimen is in poor condition and they would probably not show even if present. While clearly a coccus of *Wetherellia* the specific relationship is doubtful but the characters recall *W. variabilis* rather than *W. dixoni.*

INCERTAE SEDIS

Carpolithus curryi n. sp.

(Pl. 11, figs. 70, 71)

DIAGNOSIS. Fruit probably inferior with accrescent perianth, gamosepalous below, divided? at the apex. A syncarpous, three-loculed, loculicidal capsule, obovoid, many-seeded with axile placentation. Seeds probably in two rows in each locule borne horizontally, pointed at the hilar end, rounded at the distal end, curved? Length of fruit, 10·5 mm. ; estimated transverse diameter, 7 mm.

HOLOTYPE. V.41887.

DESCRIPTION. *Fruit:* Probably inferior with accrescent perianth, gamosepalous below, possibly dividing into free broad perianth segments at the apex of the fruit and if so segments alternating with the locules and reaching to the extreme tip of the fruit. Surface much abraded, cell structure obscure. Fruit a syncarpous capsule, approximately obovoid with three slightly unequally developed loculicidal locules indicated by lobes with a median longitudinal line of dehiscence. Surface of fruit finely striate transversely, formed of small transversely aligned cells. Placentation axile on projecting placentas. Shallow transverse furrows on the external surface of a perfect carpel indicate numerous horizontal seeds piled one upon the other probably in two rows. These impressed outlines have a slight sigmoidal curve upwards towards the plane of dehiscence. The seeds must have been narrow and pointed at the hilar end, rounded at the distal end and flattened on their contiguous surfaces, and the form suggests a curved cavity or embryo. Length of fruit, 10·5 mm. ; estimated transverse diameter, 7 mm.

Remarks. One pyritized fruit from Fisher Bed 9 with embedded sand and glauconite. It shows the perianth on one side, imperfect at the apex but suggesting a free lobe alternating with two of the locules. The upper end of one locule with seed impressions is well displayed and the ventral side of another is exposed by the loss of the dorsal wall revealing projecting axile placentas. The relationship has not been discovered but the fruit would be recognizable if found again so that a specific name, *Carpolithus curryi*, in honour of the finder has been given. It is possible that it may belong to the Monocotyledones or to Theaceae but without further evidence of seed characters no closer determination is possible.

Carpolithus sp.

(Pl. 11, figs. 72, 73)

One valve of a bisymmetric endocarp, much abraded. Obovate in outline probably with an organ at the narrow obliquely truncate end but the internal surface is too decayed to show details of the cells and their direction. Externally the margin at the broad end shows a few coarse teeth and the lateral margins show radial striations due to the alignment of obscure ill-preserved cells. A raised obovate area occupies most of the external surface but leaves a broad rim on the right. The raised area is ornamented by a rounded sigmoidal ridge which becomes thin and sharp near the base. Cell structure is obscure but a few equiaxial pits about 0·038 mm. are visible. Length of valve, 3·5 mm.; breadth, 2·8 mm.; thickness (i.e. of half fruit), 1 mm. The relationship has not been traced.

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PLATE 4

Araucarites selseyensis n. sp.

FIG. 1. Holotype. Twig showing broad spreading sometimes laterally flattened leaves. × 2·7. (V.41918.)

FIG. 2. Part ot the ventral and dorsal cuticle of a leaf from the above. The dorsal cuticle shows the tip free of stomata except for a solitary stoma separated by a belt of ordinary epidermal cells from the main left stomatal band. The leaf has been completed by a diagram based on slide V.41918*a* when perfect. *v*1 and *v*2 the two halves of the ventral cuticle split longitudinally show stomatal bands, *sb*, extending to the leaf tip. *d*1 and *d*2 are the main dorsal stomatal bands. × 50.

FIG. 3. Cone scale, upper surface with apica lprocess buried in matrix, on back of holotype. × 2·5.

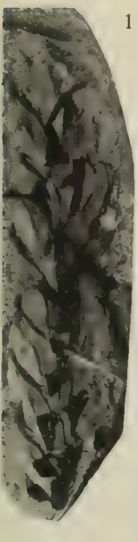
FIG. 4. Same after process, *p*, was fully exposed. Impression of lower surface here exposed by collapse of scale substance. × 2·5.

FIG. 5. Distal end of same. × 6·5.

From laminated clays and lignite equal to Fisher Bed V of Whitecliff Bay (undated lignitic phase between Cuisian and Lutetian); East Wittering.

Doliostrobus sp. (*Araucarites gurnardi* Florin)

FIG. 6. Scale for comparison. Apical process broken or buried, note greater breadth of scale. × 2. (V.17514.) Bembridge Beds ; Gurnard Bay, Isle of Wight.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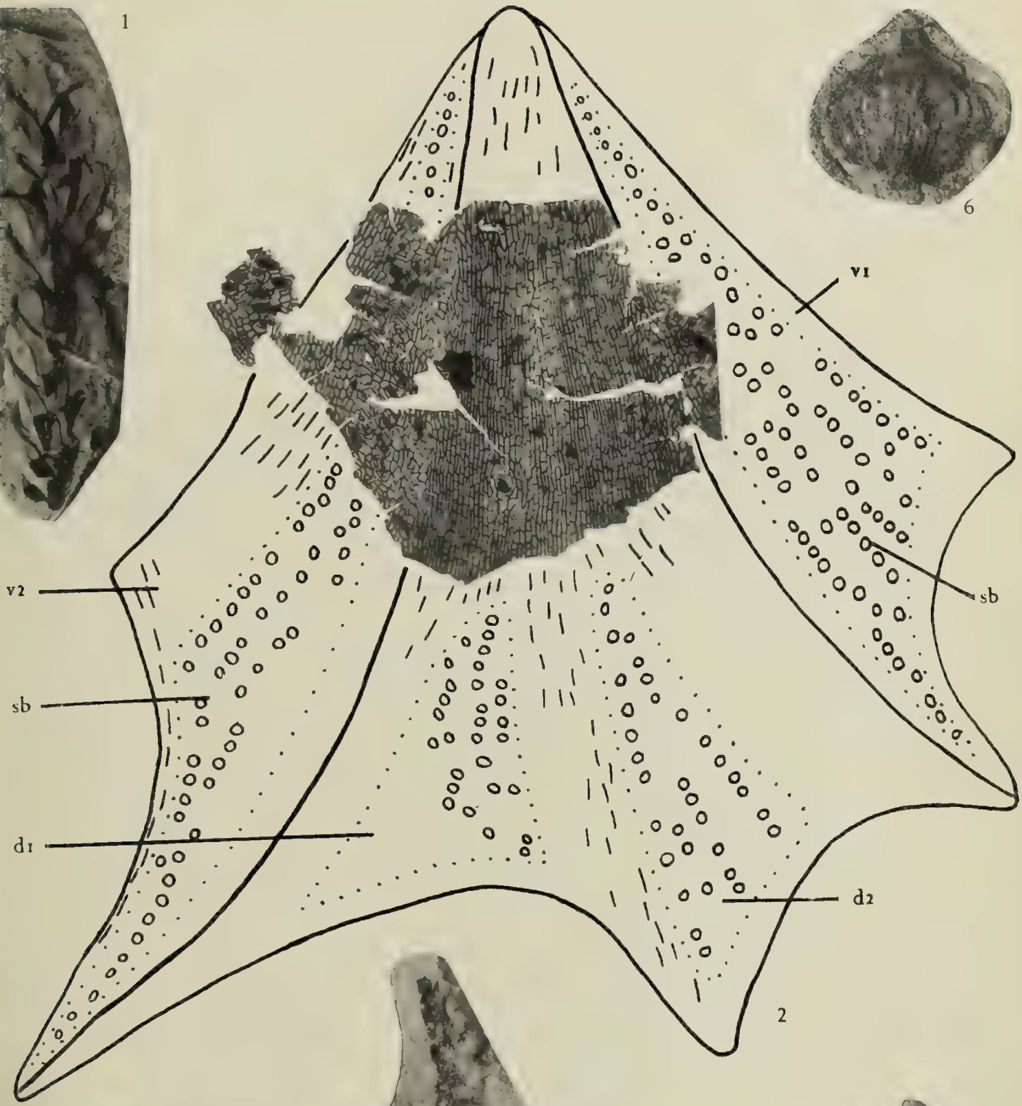
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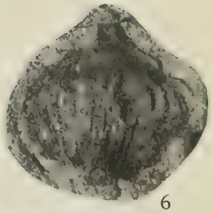
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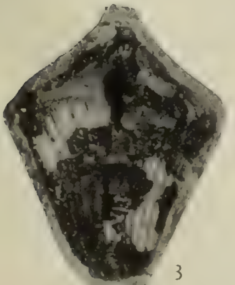
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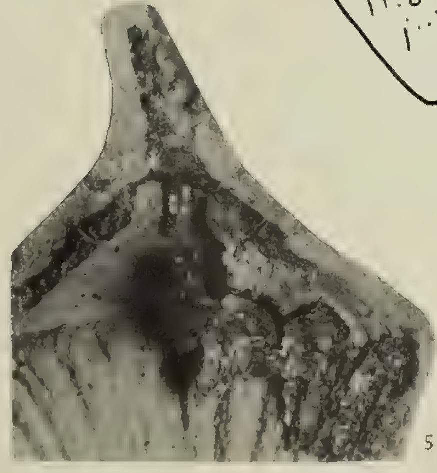
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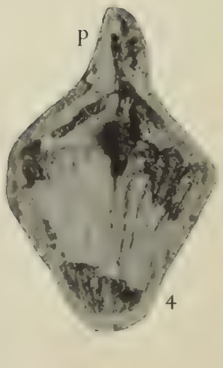

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PLATE 5

Araucarites selseyensis n. sp.

FIG. 7. Twig, one of a pair of counterparts showing acicular leaves. × 2·7. (V.41919.)

FIG. 8. Part of ventral cuticle of a leaf from the above near leaf tip showing narrow stomatal band, *sb* ; *m*, the median band of ordinary epidermal cells. × 50. (V.41919*a*.)

From grey clay (undated lignitic phase between Cuisian and Lutetian) ; East Wittering.

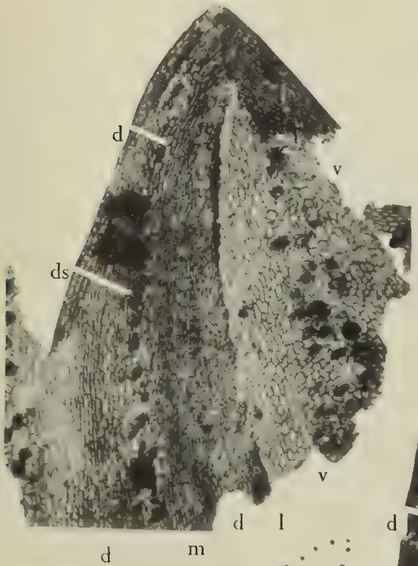
FIG. 9. Tip of a leaf from a twig in Pl. 6, fig. 13. *l*, is the sharp lateral margin ; *m*, obscure median angle on dorsal surface flanked by unequal facets. Thinner ventral cuticle with broader stomatal band is seen at *v*, *v*. Denser dorsal cuticle at *d*, *d*. A line of stomata, *ds*, is seen on one dorsal facet. There is no evidence to show whether it was continuous with the dorsal stomatal band below. × 50. (V.41920*a*.)

FIG. 10. Distal end of leaf cuticle from same twig ; *v*, *v*, ventral cuticle with stomatal band ; *l*, lateral angle of leaf between ventral and dorsal, *d*, cuticles ; *m*, median angle of dorsal surface flanked by ordinary epidermal cells without stomata. × 50. (V.41920*b*.)

FIG. 11. Ventral cuticle of a broad leaf from same twig near junction, *j*, with twig. It shows the broad median band, *m*, of ordinary epidermal cells and one broad stomatal band. Still attached is part of the dorsal cuticle, *d*. Stomata are present on this surface only below the level of the free leaf tip. × 50. (V.41920*c*.)

Horizon? In rolled clay pebble thought to be Lutetian ; Bracklesham Bay.

FIG. 12. A larger twig with spreading acicular leaves probably this species. (Now disintegrated.) × 1·8. Fisher Bed 21 or 22, opposite Medmerry Farm in beds with *Nummulites variolarius* (Auversian).



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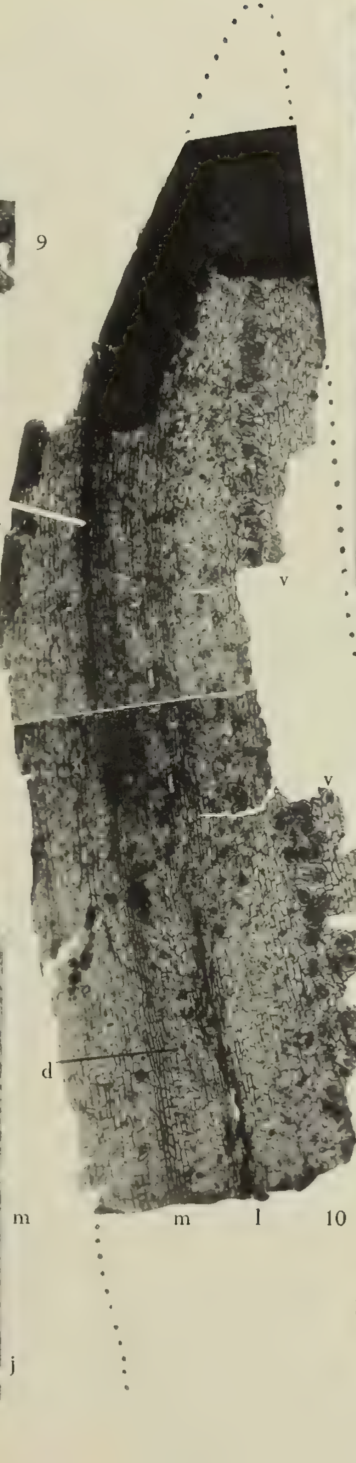

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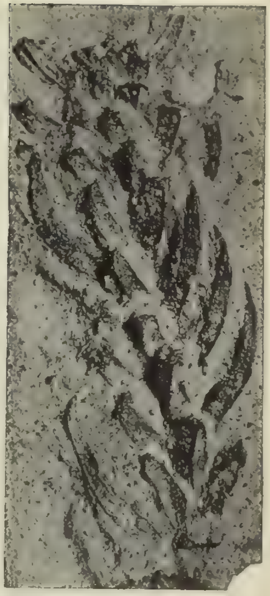

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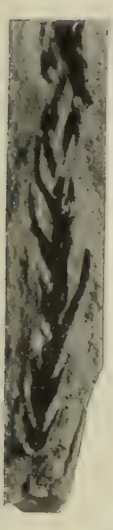

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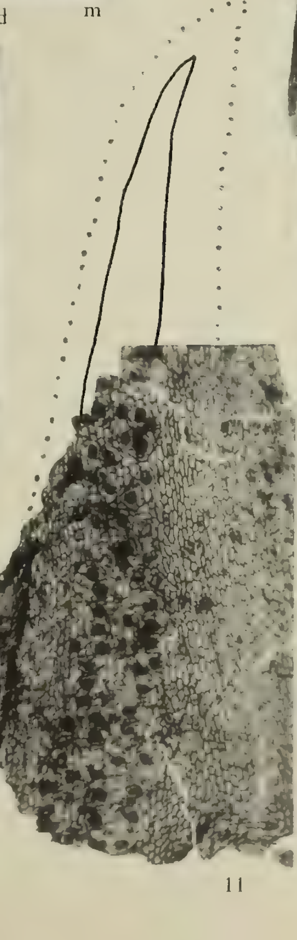

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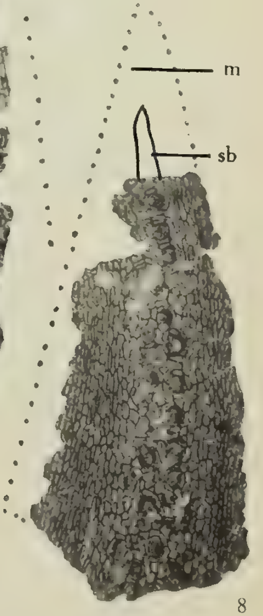

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PLATE 6

Araucarites selseyensis n. sp.

Fig. 13. Twig from which cuticles of broad and acicular leaves have been prepared. (Now disintegrated and represented by slides V.41920*a–j*.) Horizon? × 2. From rolled block thought to be Lutetian ; Bracklesham Bay.

Fig. 14. Right side of ventral cuticle near junction with twig, *j* ; *s*, stomatal band. × 50. (V.41918*b*.)

Fig. 15. Part of same to show stomata. The ordinary epidermal cells of the median band, *m*, show pits as rounded shadows. × 100. (V.41918*a*.)

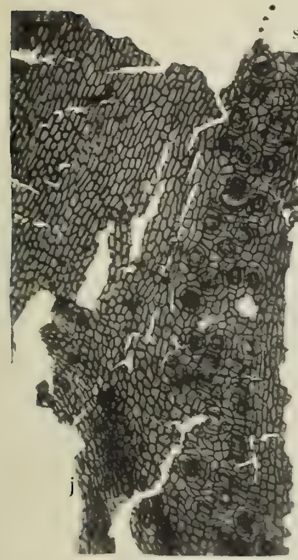
Fig. 16. Part of left ventral stomatal band of another leaf. Distortion in growth causes the stomata to be obliquely oriented. × 100 approx. (V.41918*c*.)

Fig. 17. Part of right stomatal band of same leaf with less obliquely distorted stomata. × 200 approx.

Fig. 18. Dorsal cuticle from decurrent basal part of leaf showing broad " lanes " of ordinary epidermal cells between lines of stomata. × 100. (V.41918*c*.)

Fig. 19. Part of same cuticle showing details of stomata and pits in epidermal cells. × 200 approx.

From laminated clays and lignite (undated lignitic phase between Cuisian and Lutetian) ;
East Wittering.



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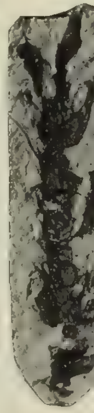

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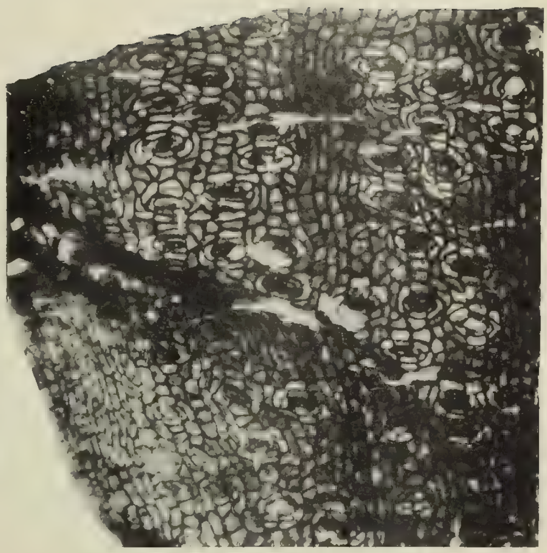

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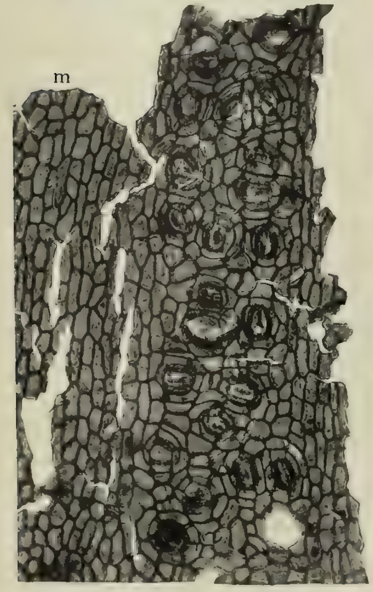

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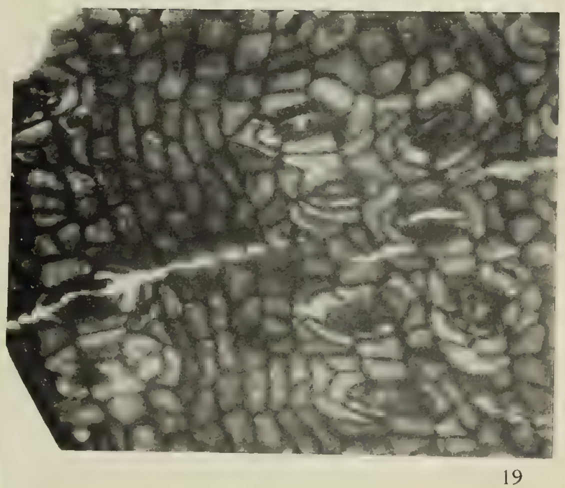

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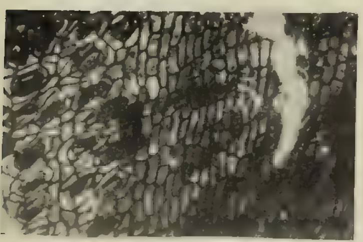

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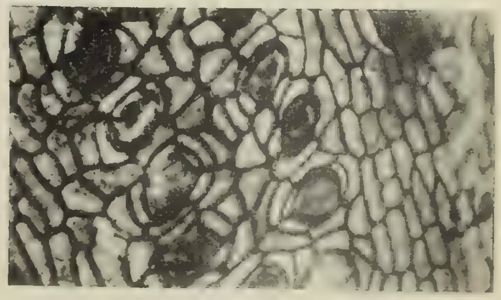

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PLATE 7

Limnocarpus forbesi (Heer)

FIG. 20. Locule cast, side. *s*, projecting hilar end of seed. Germination valve on left. ×15. (V.33813.)

FIG. 21. Same, dorsiventral view, showing gaping aperture left by the germination valve. ×15.

From Cuisian (Lower Bracklesham) ; Whitecliff Bay, Isle of Wight.

FIG. 22. Carbonaceous endocarp, side, showing *st*, style (imperfect) ; *a*, attachment and *f*, the conspicuous lateral foramen. ×15. (V.41870.)

FIG. 23. Another showing complete recurved style, *st*. Valve is in shadow at *v*. ×15. (V.41871.)

Fig. 24. A smaller endocarp. ×15. (V.41872.)

From Fisher Bed 11 or 12 (Lutetian-Auversian boundary) ; Bracklesham Bay.

Limnocarpus ? enormis n. sp.

FIG. 25. Holotype. Large endocarp with long style and tubercled surface. Gaping aperture, *k*, for fallen valve is in shadow. Long lateral foramen, *f*, is obscurely seen. ×15. (V.41874.)

FIG. 26. Another somewhat distorted endocarp, *a*, attachment. Aperture for valve at *k*, elongate lateral foramen at *f*. ×15. (V.41875.)

FIG. 27. A smaller endocarp, dorsilateral, with broad ridged valve. ×15. (V.41876.)

FIG. 28. Same, ventral, showing ridge and long style. ×15.

FIG. 29. Another with broken style, ventral. The lateral foramina flanking the ventral ridge at *f* are partly concealed by associated tubercles. ×15. (V.41877.)

FIG. 30. A very large endocarp, imperfect below. Lateral foramina concealed by tubercles are at *f*. ×15. (V.41878.)

FIG. 31. Interior of one half showing oblique ridge of condyle, *c*, corresponding with external foramina. Broken below. ×15. (V.41879.)

FIG. 32. A detached valve, side. ×15. (V.41880.)

FIG. 33. Another, dorsal. ×15. (V.41881.)

From Fisher Bed 11 or 12 (Lutetian-Auversian boundary) ; Bracklesham Bay.

Caricoidea obscura Chandler

FIG. 34. Fruit, side showing base truncated by hilar opening. ×15. (V.41884.) Fisher Bed 11 or 12 (Lutetian-Auversian boundary) ; Bracklesham Bay.

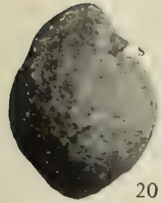
POTAMOGETONACEAE? Genus?

FIG. 35. Stem lying in matrix with leaf at node. Also internal cast of bud, *b*. *br*, a ring of bracts from which a bud has fallen. ×6·5. (V.41889.)

FIG. 36. Much puckered stem bearing clay internal casts of buds at *b*, *bb*. Basal scars are clear and an embracing bract is seen above *bb*. ×6·5. (V.41890.)

FIG. 37. Internal cast of a large bud with basal scar on right below. Two obliquely oriented stem fragments are seen above and below the bud. ×6·5. (V.41891.)

Horizon? Rolled block with *Araucarites* twig (V.41920) thought to be Lutetian ;
Bracklesham Bay.



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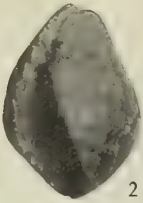

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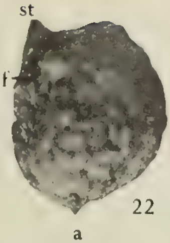

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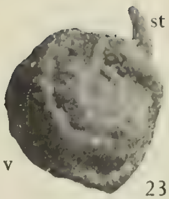

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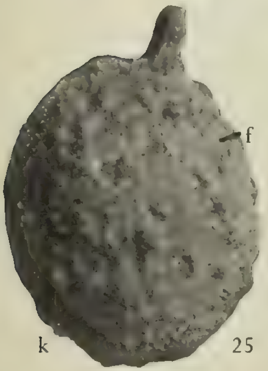

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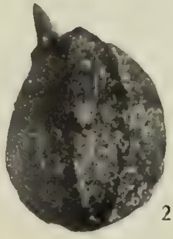

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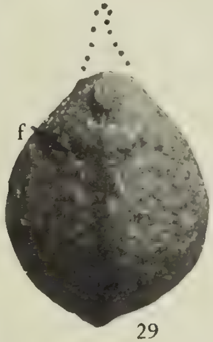

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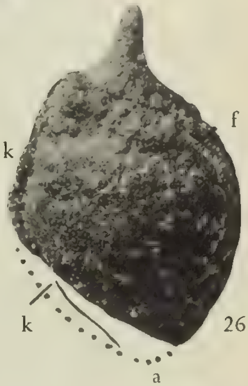

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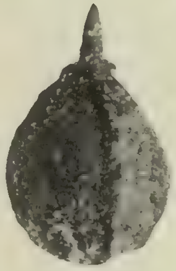

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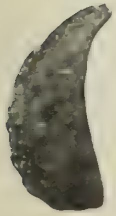

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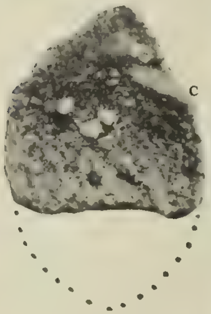

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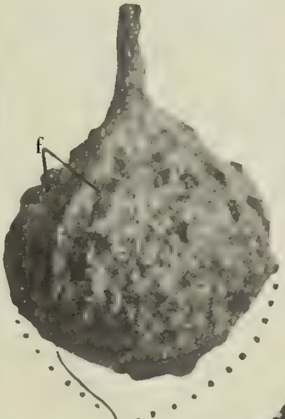

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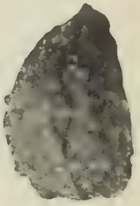

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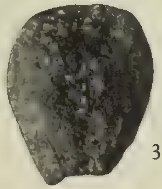

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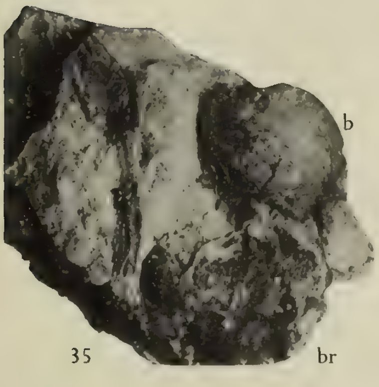

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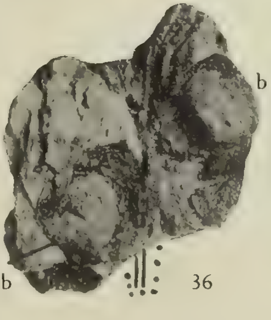

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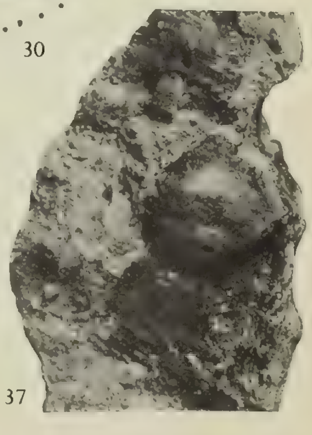

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PLATE 8

POTAMOGETONACEAE Genus ?

FIG. 38. Branched jointed rhizome, *a*, *b*, *c*, indicate branches. × 3. (V.41922.) Fisher Bed 21 (Auversian) ; Selsey.

POTAMOGETONACEAE? Genus?

FIG. 39. Striate stem showing two nodes with buds, *b*, of varying size, some still attached. Another stem with a bud lies on the extreme left of clay fragment. Persistent scales, *sc*, once surrounded a bud (now gone). × 6·5. (V.41892.)

FIG. 40. Internal cast of detached bud showing large circular attachment scar. Impressions of overlapping scales are seen on sides beyond the scar. × 6·5. (V.41893.)

FIG. 41. Another bud cast tilted to show basal scar. Fine longitudinal striae diverge from scar over sides. × 6·5. (V.41894.)

FIG. 42. Opposite end of same showing collapsed condition at apex. × 6·5.

FIG. 43. Another bud cast, side. Striate lateral surfaces are seen. Attachment scar is obscurely visible in profile at base. × 15. (V.41895.)

FIG. 44. A distorted bud showing rounded attachment scar and at the margins the serrate edges of scales in profile. × 15. (V.41896.)

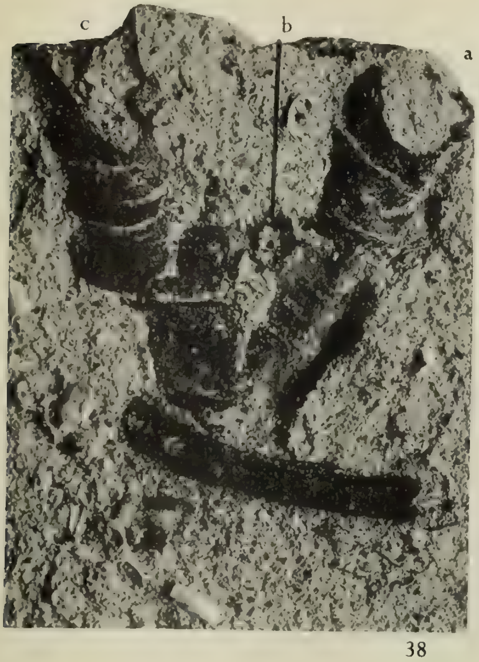
FIG. 45. Same, opposite side showing serrate edge of a scale lying obliquely. × 15.

FIG. 46. External impression of a bud, side still surrounded by carbonaceous scales. A fragment of longitudinally striate stem is seen below. × 6·5. (V.41897.)

FIG. 47. Internal cast of a bud, *b*, side, lying in a hollow in clay still flanked at base by carbonaceous scales, *s*. × 6·5. (V.41898.)

FIG. 48. Bud which appears to have begun to elongate. × 15. (V.41899.)

Horizon? Rolled block with *Araucarites* twig (V.41920) thought to be Lutetian ;
Bracklesham Bay.



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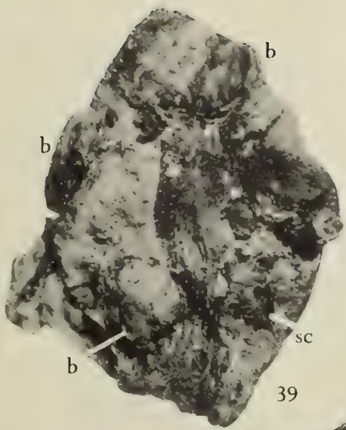

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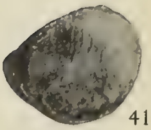

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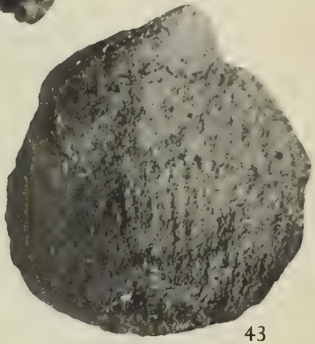

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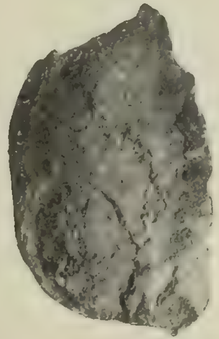

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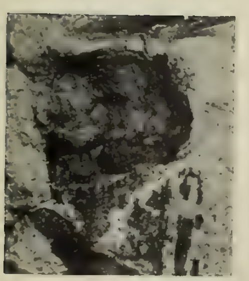

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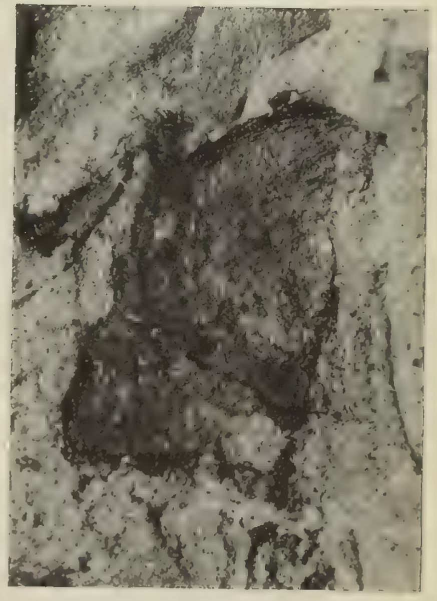

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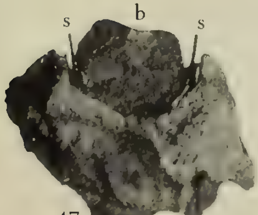

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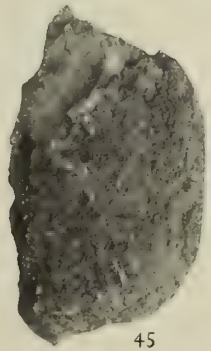

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PLATE 9

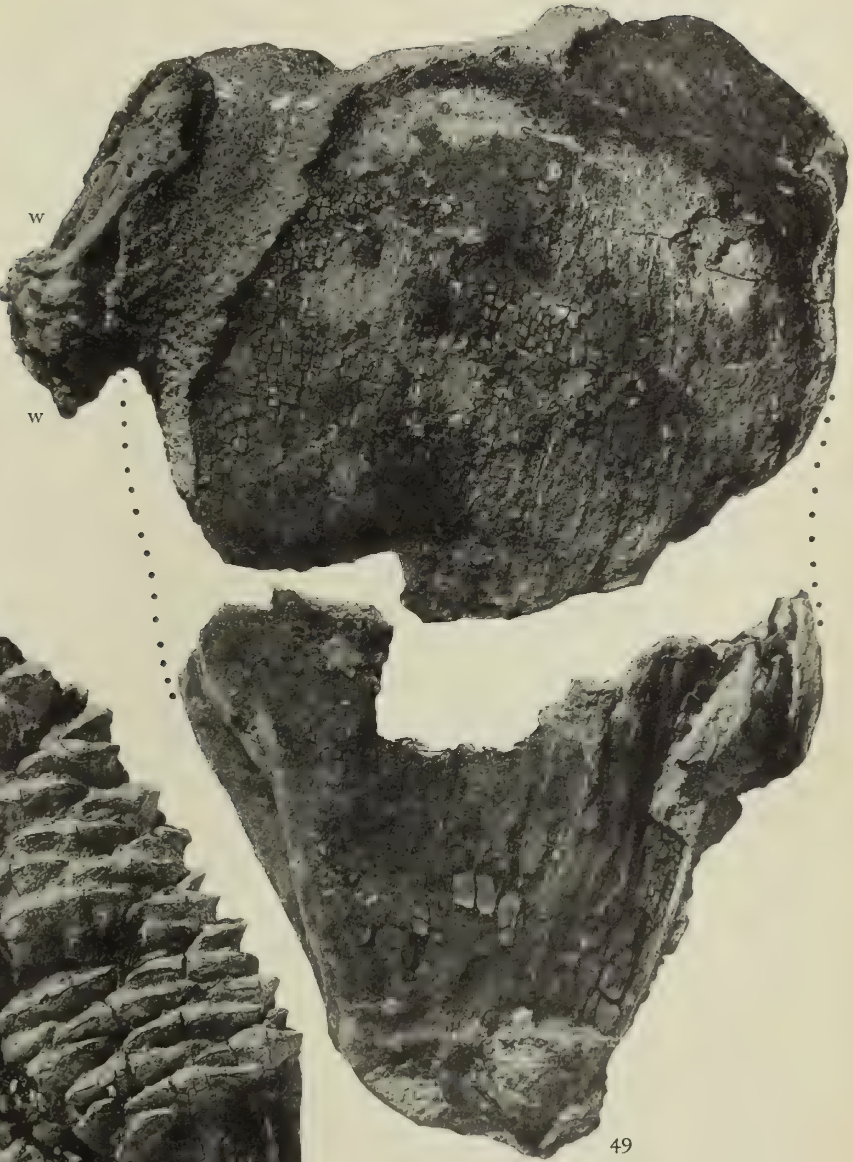
Nipa burtini (Brongniart)

FIG. 49. Large carbonaceous fruit, broken transversely and partly encrusted above with pyrites. Attached by pyrites cement at *w* is teredo-bored wood. × 0·8. (V.35722.)

Lutetian, probably from Fisher Bed 7 or 8 ; Bracklesham Bay.

Pinus bowerbanki (Carruthers)

FIG. 50. Cone, imperfect below, showing the narrow apophyses with marked transverse carina. × 0·9. (V.3313.) Bracklesham Bay.



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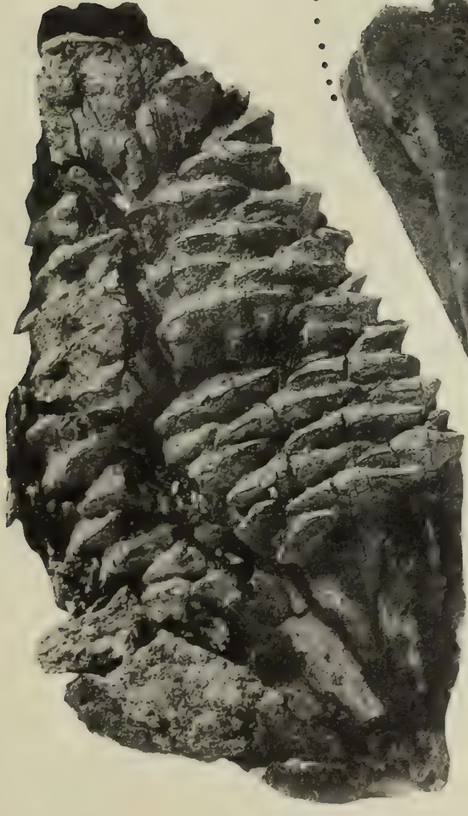

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PLATE 10

Nipa burtini (Brongniart)

FIG. 51. Flattened immature pyritized fruit. ×1. (V.29214.)

FIG. 52. Larger imperfect fruit incomplete at base and apex, showing in profile aperture for germination. Fibres of sarcocarp show on sides. ×1. (V.40260.)

From Fisher Bed 4 (Palate Bed) (Lutetian); Bracklesham Bay.

FIG. 53. Minute immature fruit with exocarp preserved embedded in glauconitic ferruginous sand with abundant remains of *Nummulites laevigatus*. ×2·7. (V.33732.)

Lutetian, most probably from Fisher Bed 6; Bracklesham Bay.

Laurocalyx sp.

FIG. 54. Cupule, slightly distorted so that the rim of the cup is exposed all round. ×6·5. (V.41885.)

FIG. 55. Same, opposite side. ×6·5.

Loose on shore near Fisher Bed 7 (Lutetian); Bracklesham Bay.

Wetherellia dixoni (Carruthers)

FIG. 56. Holotype, fruit, apex. ×2. (40509.)

FIG. 57. Same, base, showing casts of spine bases as light coloured spots. ×2.

FIG. 58. Same fractured longitudinally. On left of axis is a septicidal surface with fibres from the axis; on the right a locule with impression of distorted pendulous seed. ×2·8.

FIG. 59. Same showing oblique dorsiventral compression. Two locules are exposed. Passage of funicles from axis to seeds is shown. Spine bases in thickness of wall appear white through partial decay of pyrites casts. ×6·5.

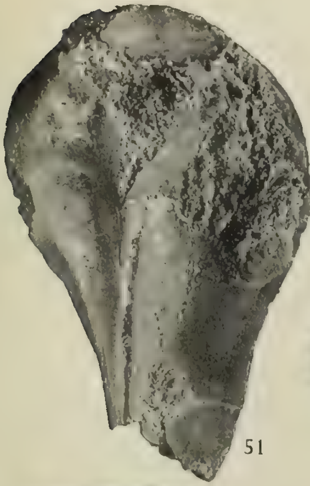
FIG. 60. A seven-carpelled fruit with marked alternating ribs and furrows. Incipient splitting is seen at the base. ×2·8. (V.33827.)

FIG. 61. Same apex. Spines represented by pyrites casts of their hollow bases worn down to surface level. × 2·8.

FIG. 62. Same side, showing dorsiventral crushing. ×2·7.

FIG. 63. Same, split loculicidally. In right locule a minute immature pendulous seed is visible. There is a developed but distorted seed in the left locule. ×2·7.

Loose on shore, Bracklesham Bay.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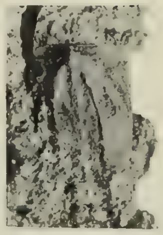
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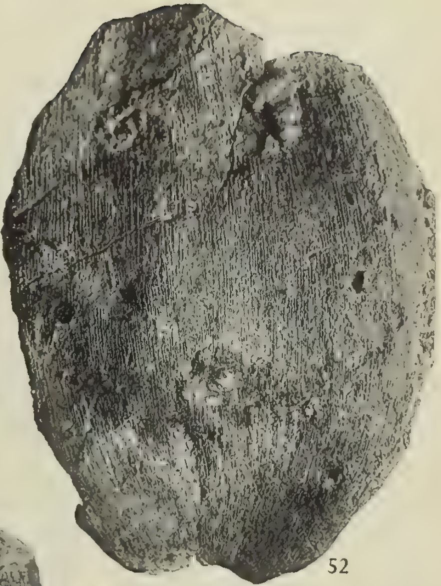
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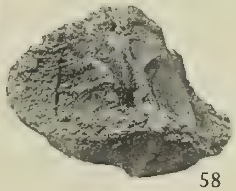
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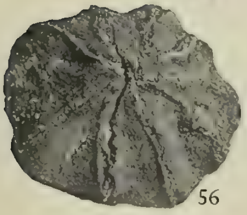
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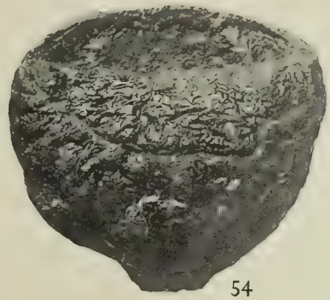
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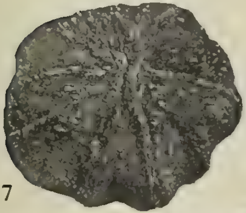
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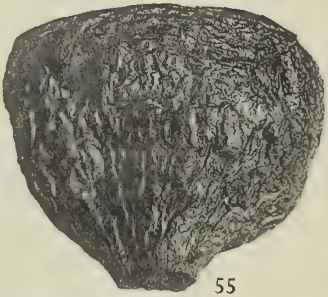
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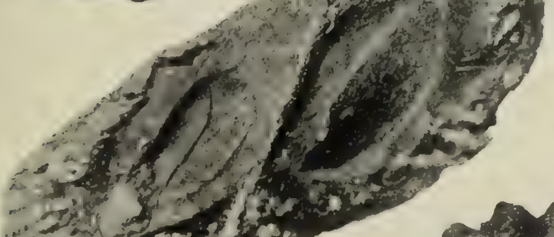
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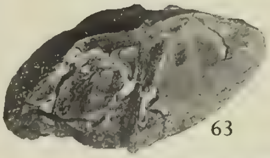
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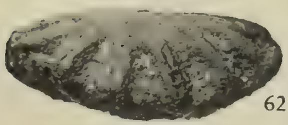
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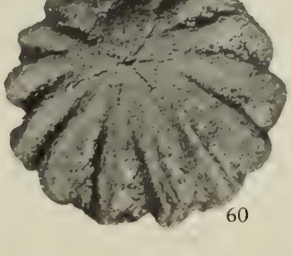
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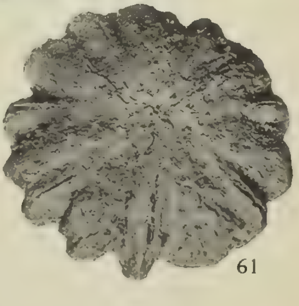
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PLATE 11

Wetherellia dixoni (Carruthers)

FIG. 64. Base of six-carpelled fruit, asymmetrically developed and obliquely compressed. Shows incipient splitting. × 2·8. (V.33825.)

FIG. 65. Same, apex. × 2·8.

Loose on shore, Bracklesham Bay.

Wetherellia sp. (? *W. dixoni* (Carruthers))

FIG. 66. External cast of a coccus. The apex is truncated obliquely by the fracturing of the stone, casts of spines show as small white circular scars. × 2·5. (V.35718.)

FIG. 67. The carbonaceous coccus from the above (similarly truncated), external surface. The longitudinal angle marks the plane of loculicidal dehiscence. × 1·7.

FIG. 68. Same, septicidal surface, showing axial fibres with a branch diverging over the right septicidal surface and itself branching again. × 1·7.

From Cakeham Beds A (Cuisian) ; opposite West Wittering Beacon.

Wetherellia variabilis Bowerbank

FIG. 69. Much broken coccus, inner septicidal surface showing median line of loculicidal dehiscence. × 2·8. (V.41886.) Fisher Bed 2 (*Turritella* Bed) (Lutetian) ; Bracklesham.

Carpolithus curryi n. sp.

FIG. 70. Battered pyritized fruit, side. The carpel facing the camera has lost its outer wall so that the placentas, *p*, are exposed, showing attachment scars of numerous seeds. Carpel seen in profile on the left shows impressed through the walls the horizontally attached and oriented seeds within. Carpel on right irregularly broken. × 6·5. (V.41887.)

FIG. 71. Same, apex. Locule on left in Fig. 70 is at *l*. Placentas in broken locule are at *p*. A perianth segment, *s*, is seen extending to the apex of the fruit over the third imperfect locule. × 6·8.

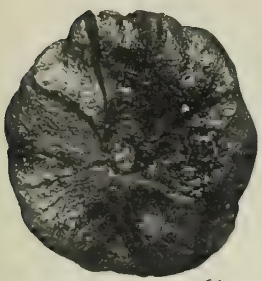
From Fisher Bed 9 (*Ostrea tenera* Bed) (Lutetian) ; Bracklesham Bay.

Carpolithus sp.

FIG. 72. Valve of a fruit, decaying external surface. × 6·5. (V.41888.)

FIG. 73. Diminished outline drawing to elucidate features now obscured through decay.

From Fisher Bed 21 (Hard Bed) (Auversian) ; Selsey.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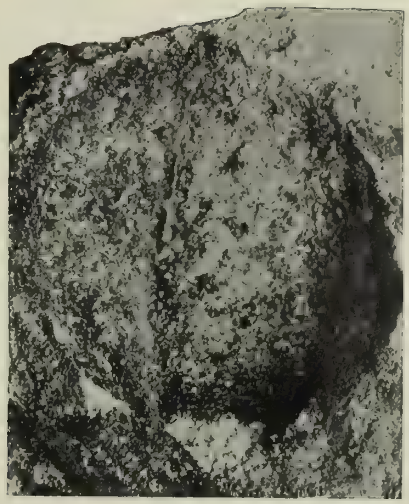
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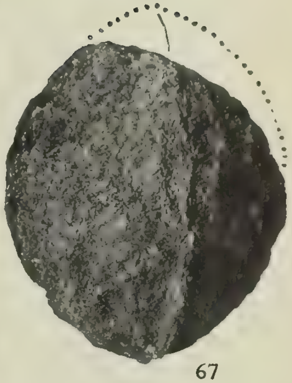
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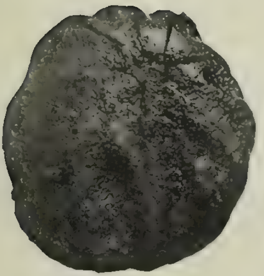
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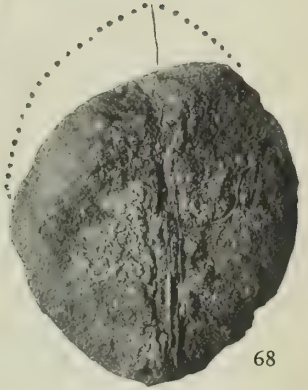
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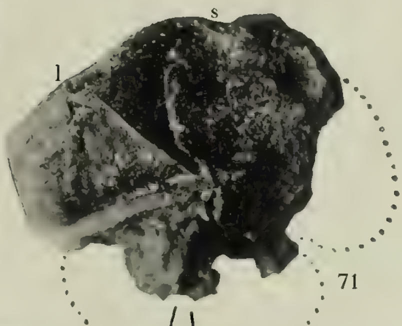

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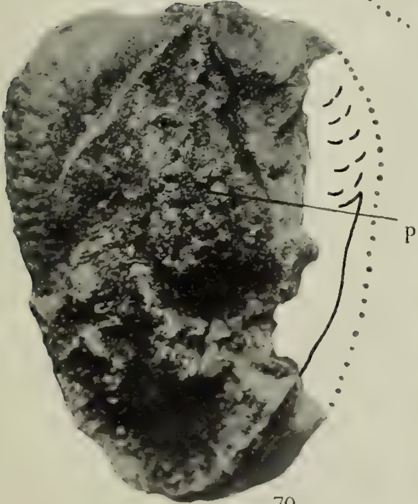

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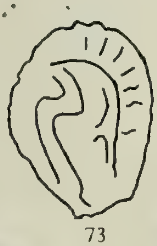
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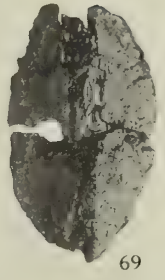
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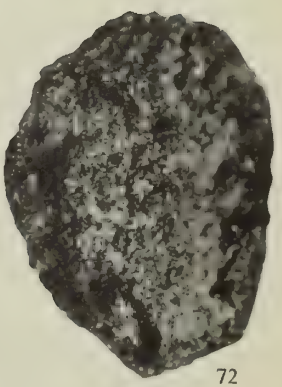
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NOTES ON EOCENE TARSIOIDS AND A REVISION OF SOME NECROLEMURINAE

E. L. SIMONS

BRITISH MUSEUM
23 MAR 1961
NATURAL HISTORY

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THE BRITISH MUSEUM (NATURAL HISTORY)
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LONDON: 1961

NOTES ON EOCENE TARSIOIDS AND A REVISION OF SOME NECROLEMURINAE

BY

ELWYN L. SIMONS

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BRITISH MUSEUM
23 MAR 1961
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Pp. 43–69; *Pls.* 12–14; 3 *Text-figures*

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NOTES ON EOCENE TARSIOIDS AND A REVISION OF SOME NECROLEMURINAE

By E. L. SIMONS

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SYNOPSIS

In this paper the problems of the relationship of European Eocene Necrolemurinae to each other and to contemporaneous and later Primates are considered. A re-affirmation of tarsioid affinities is made for this group, and it is ranked together with Tarsiinae in the family Tarsiidae. Evidence substantiating resemblances in dental formulae, tooth cusp patterns, auditory construction, and cranial osteology between tarsiines and necrolemurines is presented. *Pseudoloris* is assigned to the Necrolemurinae and the taxonomy of *Nannopithex* is revised. In conclusion, a number of dental similarities between necrolemurines, omomyids and North American anaptomorphids (as defined by Gazin, 1958) are evaluated.

ABBREVIATIONS

A.M.N.H., American Museum of Natural History, New York
B.M.N.H., British Museum (Natural History)
G.P.I.H., Geological and Paleontological Institute, University of Halle-Wittenburg
Montauban, Natural History Museum, Montauban, France
M.C.Z., Museum of Comparative Zoology, Harvard University
Paris, National Museum of Natural History, Paris
P.U., Princeton University

I. *NECROLEMUR ANTIQUUS* FILHOL, AN EOCENE TARSIOID PRIMATE

The Eocene necrolemurine primate *Necrolemur antiquus*[1] from the Quercy phosphorites and possibly of early Ludian age, has long been thought to be a typical tarsioid primate. Indeed, this form has been one of the primary bases for the hypothesis that many of the small Eocene Primates of Europe and North America can correctly be called tarsioid, in that its characters link it and thereby some other Eocene Primates, in particular the necrolemurines, with the living *Tarsius*. Gregory (1915 : 30) has given some of the reasons for this placement of the group as has Simpson (1940 : 198) for *Pseudoloris*, here assigned to the necrolemurines, and the case for affinities with *Tarsius* has been most recently expressed by Gazin (1958 : 99).

In view of Hürzeler's conclusion (1948) that *Necrolemur* is a lemuroid primate the investigations presented in this paper were undertaken at the suggestion of Sir Wilfrid Le Gros Clark.

The lemuroid interpretation. Hürzeler (1946, 1948) stated that the structure of the skull of *Necrolemur* (principally the auditory region) as seen in Montauban 9, is lemuroid, and that this primate exhibited no special resemblance to *Tarsius* that could justify calling it a tarsioid. This opinion, which was in part suggested by the material examined by him, considerably affected subsequent thinking on primate taxonomy and it is advisable to consider here in some detail the construction and placement of the tympanic ring of *Necrolemur* together with the significance of this structure in the reconstruction of the phylogeny of Primates. Hill's comments (1955 : 293) are fairly typical of the reaction to Hürzeler's observations.

> " Hürzeler has dissected the bulla of one specimen and finds, surprisingly, that the interior does not resemble that of *Tarsius*, but agrees rather with that in Malagasy lemurs and of *Adapis*. He disproves the conclusion of Stehlin that the annulus tympanicus (ectotympanic) is fused with the bulla, for he declares it to be quite freely suspended in the tympanic cavity. Moreover, it is not a simple ring, such as occurs in the fossil Malagasy types, but expanded into a plate-like form, attached below and laterally to the inner end of the osseous meatus."

Since Hürzeler's suggestion that *Necrolemur* is lemuroid there has been a tendency to maintain that a distinction between lemuroid and tarsioid types cannot be made among early Tertiary primate species. This view was expressed by Simpson (1955 : 438) as follows :

> " The majority of Eocene genera have at one time or another been considered ' tarsioid.' Re-study of some, especially those represented by skulls or other relatively good material has resulted in their transfer to the ' lemuroids.' . . . *Nannopithex*, *Necrolemur* and *Microchoerus* (see Hürzeler, 1948)

---

[1] Determinations on the cranial anatomy of *Necrolemur antiquus* are facilitated by the relatively large number of skulls of this species which are available for study in the following European and North American museum collections : Basel number Q.H. 470, Montauban 9, Paris Museum (five skulls), British Museum M3747 and M4490. Museum of Comparative Zoology, Harvard University, M.C.Z. 8879, and at Princeton University, P.U. 11465. I have studied all these specimens excepting Montauban 9. Stehlin (1916) also mentioned two skulls in the collections of the Faculty of Sciences at Marseilles.

> are examples particularly to the point. Still the mass of ' Anaptomorphidae ' (probably not a natural family even after recent removals) has continued to be labelled ' tarsioid.' The fact is that there is no convincing evidence that any early primate is more ' tarsioid ' than ' lemuroid ' in natural affinities."

Simpson (following Hürzeler's assignment of the necrolemurines to the Lemuroidea) was correct in suggesting that the term tarsioid was no longer meaningful. *Necrolemur* and its allies had been thought to have more resemblance to *Tarsius* than any other European or North American early Tertiary primate stock.

It is possible to question on various grounds whether the Necrolemurinae should be called tarsioids, even if one believes that the evidence for their close association with the ancestral line of *Tarsius* is sound. It is not possible, however, to assign the necrolemurines to the Lemuriformes as Piveteau (1957 : 64–71) has done while leaving all the much less *Tarsius*-like North American " anaptomorphs " ranked with the Tarsiiformes. No other early Tertiary primate is more convincingly tarsioid than *Necrolemur*.

MORPHOLOGY

Ectotympanic.—Hürzeler's view is most clearly stated (1948 : 28) in a section beginning, " Das Verhalten des Annulus tympanicus von *Necrolemur* entspricht prinzipiell jenem von *Adapis* . . .". The accompanying Plates 12 and 13, of the annulus tympanicus of *Necrolemur*, B.M.N.H. M4490 (from Mouillac, France) and Plate 14 of *Adapis parisiensis*, B.M.N.H. M1345 (from Caylux, France), are sufficient to show that these two forms have little if any significant similarity in the position and relationships of the ectotympanic element. Stehlin (1916 : 1352) also stressed this difference remarking : " Das Verhalten des Annulus tympanicus ist somit bei *Necrolemur* ein ganz anderes als bei *Adapis* ". In *Adapis* the annulus lies within the bulla, it is free, and there is no bony external auditory meatus whatever in specimens examined by me. In these regards the annulus tympanicus of *Adapis* corresponds closely to the situation of this bone in the great majority, if not all, of the living members of the Lemuriformes, e.g. *Daubentonia* and *Lemur*. It would, perhaps, be tedious to recite how often the free, ring-like tympanic has been given as a character of the Lemuriformes ; van der Klaauw (1931 : 12) listed about thirty page-references to this effect for various living and fossil lemuroids (including *Adapis* and *Notharctus*). In some living prosimians, other than *Tarsius*, such as *Perodicticus* and *Lemur*, a slightly developed bony external meatus has been reported, but it is not truly tubular (see van der Klaauw, 1931 : 155–156).

Unlike any living lemur or loris, *Necrolemur* has a remarkably long bony external meatus (typically longer than that of *Tarsius*) which is fused to the bulla internally. The latter feature can clearly be determined by examination of the internal posterolateral part of the ventral bulla wall of *Necrolemur* in B.M.N.H. M4490. The conclusion that the structure applied and fused to the ventrolateral bulla wall (see Plates 12 and 13) is the inner end of an expanded and tubular annulus seems inescapable. It is not very difficult to reconcile this observation with the figures and discussion in Hürzeler (1948). I interpret the scalloped areas seen in the region of the anterointernal margin of the ventral side of the annulus of Montauban

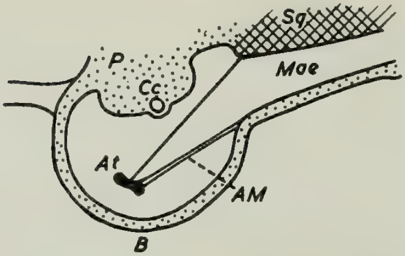

FIG. 1a Cross sectional diagram of auditory bulla of Necrolemur antiquus (after Hürzeler, 1948, fig. 29.)

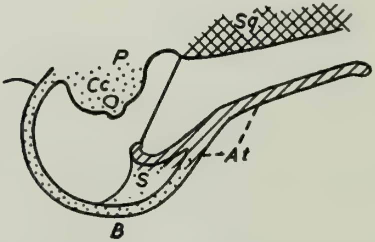

FIG. 1b Diagram of cross section of auditory bulla of Necrolemur antiquus (Brit. Mus. Nat. Hist. no. M 4490.)

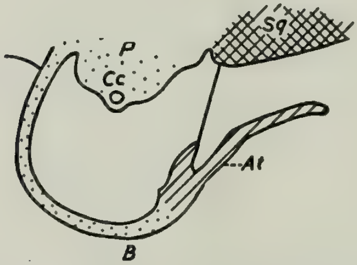

FIG. 1c Cross sectional diagram of the auditory bulla of Tarsius spectrum (Princeton Univ.. ost. coll. no. 375.)

P–Petrosal B–Bulla Cc–Carotid canal At–Annulus tympanicus
A M–Annulus Membrane Mae–Ext. auditory meatus Sq–Squamosal
S–strut joining tympanic ring and bulla wall

9 (see his figure 27) as the bases of the struts which connect the expanded ring and bulla wall in this area. In *Necrolemur* the annulus consists of a thin lamina of bone partly fused to and partly composing the ventral wall of the bulla in the region of the internal end of the external bony meatus, turning up from the internal surface of the bulla along its mesiad margin. This internal free margin of the ring (the direct support of the tympanum) is, at intervals, further secured to the ventral bulla wall by struts (six are visible in B.M.N.H. M4490, four in M.C.Z. 8879 and one in P.U. 1165), most of which run parallel to the main axis of the bony external meatus. These struts do not occur in *Tarsius* or in any other primate described to date. Nevertheless, *Necrolemur* exhibits a real resemblance to *Tarsius* in the fusion of the ring with the bulla wall and in the lengthening of the bony meatus. In *Tarsius spectrum* a ridge projects from the inside of the ventral bulla wall running around the circumference of the ear drum upon which the tympanum is stretched. This, as in *Necrolemur*, is the internal free margin of the ring. The main difference from *Necrolemur* being that this ridge or margin is inclined more laterally.

The conformation of the annulus tympanicus suggested for *Necrolemur* is indicated in Text-fig. 1, which compares a cross-section of the auditory bulla given in Hürzeler (1948, fig. 29) with that of B.M.N.H. M–4490, and of *Tarsius spectrum*. As can be seen in Plate 13, it is possible to trace continuous bone from the left hand margin of the removed part of the bulla wall (at A) to the remaining fragment of the external bony meatus (at B). Evidently the plate-like area in the centre of this figure corresponds to the part of Montauban 9 referred to by Hürzeler as the " Annulus-Membran ". This structure is clearly ossified and would appear to be more reasonably considered as part of the expanded annulus. There is clearly a continuum of bone between the internal free margin of the annulus and osseous meatus. Possibly the expanded and fused ring in the ancestry of both *Tarsius* and *Necrolemur* arose initially by a spreading of the ossification centre of the ectotympanic through the annulus membrane and outward to form a tubular meatus. Whatever the origin, the end result is very similar in these two Primates. Hill (1955 : 9) has summed up the conventional view as to the significance of an expanded tympanic ring for primate taxonomy as follows :—

> " The tympanic bone [in ' haplorhine ' primates] is very variable, but the specialized lemurine condition, where the annulus is enclosed within the bulla, never occurs. In tarsioids and catarrhines the ring is produced outwards in the form of a bony tube (osseus meatus), but in Platyrrhini the lorisoid condition persists, i.e. with the annulus exposed and contributing to the formation of the wall of the bulla (van Kampen, 1905) ".

Hürzeler (1948 : 29) cites Lorenz von Liburnau (1905) as a source for statements about a tubular ectotympanic in *Megaladapis* but the latter's comments are vague and capable of more than one interpretation (van der Klaauw, 1931 : 33). Of further interest in this regard is van der Klaauw's discussion of the false external auditory meatus, or meatus spurius, formed when the glenoid region is shifted posteriorly and abuts against the mastoid (or post-tympanic process) thus constituting a ventral bridge between the bulla and external auditory opening. Such a squamosal-mastoid arch is sometimes present in *Nycticebus* and similar occurrences may account for some of the reports of expanded ectotympanics in Lorisiformes. The derivation of the bony external meatus in prosimians can be of several different kinds. In tupaiaoids (*Dendrogale*) an entotympanic meatus, in some lemurs and lorises a partial contribution from the squamosal (meatus spurius), and a true or tubular bony meatus, which in *Tarsius*, cercopithecoids and hominoids is derived from the ectotympanic. Comparison of forms such as *Loris* or *Nycticebus* with *Tarsius* or *Necrolemur* at once shows how different these two types of progressive prosimians are in this region.

Auditory bullae of several well-preserved specimens of *Megaladapis* in the British Museum (Natural History) and in the American Museum of Natural History show that this genus exhibits a partial meatus spurius, but most sutures between the bones involved are closed. The arcuate bony attachment for the tympanum in *Megaladapis* (A.M.N.H. 30024) lies high on the dorsal face of a rather large bullar cavity (near the promentorium) and from it a sheet of bone fans out dorsolaterally, apparently an ossified annulus membrane. In complete contrast with *Necrolemur* the internal free margin of the ectotympanic extends through the spurius meatus surrounding it. However at the margin of the auditory aperture lies a partially separate, rugose bony rim. This rim is presumably the outer end of an ectotympanic tube (see Lorenz, 1905 : 463). Whatever the exact relationships with surrounding bones are, and these are obscured by closure of sutures, the ectotympanic of *Megaladapis* has no resemblance to that of *Necrolemur*. In fact, the appearance of the auditory region seems about as different in these two genera as could be expected for two mammals referable to the same order. Nor does the morphology of this part of the skull suggest any special affinity between them.

Hürzeler's view, that the annulus and osseous meatus in *Megaladapis* and *Necrolemur* are similar, even if tenable, would hardly provide relevant information for the assignment of the latter to the Lemuroidea. Rather, it emphasizes an aberrant feature of *Megaladapis*, a form which (together with a few little-known allied genera) has long been known to exhibit many characters divergent from the remainder of Malagasy Primates (Hill 1953 : 655). On the basis of a single feature, the conformation of the tympanic annulus, it cannot, of course, be asserted that similarities in its make-up relate *Necrolemur* and *Tarsius*, any more than one can say that a tubular construction of this bone relates *Necrolemur* and *Megaladapis*. If it were not for the many other characters shared by *Necrolemur* and *Tarsius* (see Table I, p. 52) ectotympanic resemblances between any two of the three could be ascribed to parallelism. Two conclusions suggested by the relationships discussed above are : 1) that *Megaladapis* in the region of the external auditory meatus diverges from both living Lemuroidea and from *Necrolemur* and 2) that *Necrolemur* exhibits a tubular osseous meatus not unlike that to be expected for an Eocene member of the particular stock from which *Tarsius* arose (Text-fig. 1).

Compared with living and post-Eocene Primates the structure of the ectotympanic of *Necrolemur* is more " advanced " than in any other known prosimian except *Tarsius*. Of course, demonstration that the centre of ossification of the external auditory meatus in *Necrolemur* lies in an embryonic horseshoe-like ectotympanic is not possible for this fossil species. Such a ring-like structure does precede the tubular conformation in *Tarsius.* Consequently in the latter, this manner of development justifies reference to the tubular structure as part of the ectotympanic. Although developmental history is not known for *Necrolemur,* there is certainly nothing in the conformation of the annulus of the known adults to prove that it did not arise much as in *Tarsius.*

The only other fossil prosimian known to have a tubular bony meatus is *Plesiadapis.* A skull of this primate recently described by Russell (1960 : 312–314) found near Cernay, in French continental late Paleocene beds, shows that this form has an extremely long osseous auditory meatus. Considering the very great differences between *Necrolemur* and *Plesiadapis* in the remainder of their cranial anatomy, the conclusion that this feature in common is due to parallelism seems almost unavoidable. Moreover, instead of standing out from the skull base, as in *Necrolemur* and *Tarsius,* the osseous meatus of *Plesiadapis* is sunk between the adjoining bones, as in *Galeopithecus.*

Entotympanic and entocarotid circulation.—Hürzeler (1948 : 29) was unable to find a suture between the petrosal and bulla in *Necrolemur* and implied that this ranked it definitely with Lemuroidea and not Tarsioidea. However, van der Klaauw (1931 : 285) indicates that the bulla arises in the latter group in the same manner as in lemurs. The presence of a separate centre of ossification for the bulla in tupaiaoids is now well established, but in the remaining Prosimii it apparently always arises from the petrosal. Consequently, the absence of a suture between bulla and petrosal does not distinguish lemuriform from tarsiiform Primates, and is equivocal here. It is, perhaps, not accurate to speak of prosimians, other than tupaiaoids, as having an entotympanic, but van der Klaauw (1931) considers that the entotympanic, when continuous with the bulla has simply lost its independence as an ossification centre.

Gregory (1915 : 430) was able to deduce from the positions of the entrance and exit of the carotid artery on the bulla that *Necrolemur* resembled *Tarsius* and not other prosimians in entocarotid circulation. Hürzeler's illustrations (1948, figs. 30, 31) confirm Gregory's suggestion of tarsioid affinities, by showing that his posited course for the entocarotid was correct and that the stapedial branch is smaller than the promentory artery, as in *Tarsius.* In *Tupaia* and those lemurs in which the carotid enters the bulla the reverse is the case (see Saban, 1957, fig. 36). There are, of course, the expected differences (between the Eocene and the living tarsiids) in the exact route of the entocarotid artery but such distinctions in *Necrolemur* do not approximate the Lemuroidea to any appreciable degree.

The tarsioid characters of Necrolemur.—Table I lists those features shared by necrolemurines and *Tarsius,* particularly those not occurring or seen only sporadically in Recent and fossil Lemuriformes and Lorisiformes. The limitations of tabular expression prevent detailed citing of sources (and partial exceptions) ; other students have, and may again assess some of these characters differently. Although opinions vary as to individual features it does not seem possible to question any longer that the complex, or nexus, of shared osteological details in necrolemurines and tarsiines justifies their close taxonomic association. Particularly to the point in this regard are the remarks of Gregory (1920 : 193) on the amount of variability in morphology allowable within a single mammalian family. Many cranial similarities between *Tarsius* and *Necrolemur* can be attributed to parallelism, but to explain all those listed (and others not amenable to tabular presentation) in this manner would be to assert the impossibility of distinguishing between real evolutionary affinities and parallelism. Such an agnostic attitude does not seem justified in this case. Moreover, in mammalian palaeontology it is almost always easier to produce an argument favouring separation of two given groups than it is to prove their valid

TABLE I. A COMPARISON OF LEMUROID AND TARSIOID CHARACTERS

CHARACTER	LEMUROIDS		TARSIOIDS
	Lemuriformes (Lemuridae and Adapidae)	Lorisiformes	Tarsiiformes (Tarsiinae, and Necrolemurinae)
1. Lower canine	shorter than upper or incisiform	incisiform	longer than upper
2. Zygomatic arches	typically stout (flaring)	variable (flaring)	slender (close to skull)
3. Postorbital opening (area)	large	rather large	almost closed or small
4. Brain case (transversely)	very narrow to expanded	expanded	much expanded
5. Muzzle (length)	long	long to medium	very short
6. Muzzle (width)	typically broad	variable	very narrow
7. Contact between jugal and lacrymal	typically occurs	often occurs	does not occur
8. Ectotympanic (position)	in bulla	at margin of bulla	extends out of bulla
9. Ectotympanic (shape)	annular	annular but broad	tubular
10. Elongation of calcaneum and astragalus	none	some	some
11. Inflation of bullae	typically inflated	little inflation	much inflation
12. Bony canal of promontory artery	small, in bulla	not ossified not in bulla	large, in bulla
13. Median lacerate foramen	variably present	present	not present
14. Carotid foramen	at posterolateral angle of bulla	not present	on ventromedial face of bulla
15. Septum between tympanic cavity and hyptotympanic sinus	incomplete	complete	incomplete
16. Tibio-fibula	does not occur*		may occur in both subfamilies
17. Palate	broad anteriorly		narrow anteriorly
18. Tooth rows	parallel (U-shaped)		converge (V-shaped)
19. Upper canine	much larger than ant. incisor		smaller than ant. incisor
20. Molar hypocone	variable but often large		often small
21. Posterior nares (shape)	broad		narrow
22. Position, posterior nares	anterior to M^3		well behind M^3
23. Pterygoid alae	long anteroposteriorly		short anteroposteriorly
24. Bullae (position)	well separated		approximated anteriorly
25. Mastoid region	little or not inflated		inflated
26. Direction of foramen magnum	largely backward		largely downward
27. Posterior palatine torus	absent		present
28. Contact of external pterygoid alae with bulla	touching		broadly overlapping
29. Interfrontal suture	typically remains open in adults		fused in adults

* Characters following 15 are typical of both Lemuriformes and Lorisiformes.

association. Fortunately, in the case of *Necrolemur*, preservation of almost every part of the skull allows for more precise judgements of affinity than is usually possible for a fossil primate.

In summary, that *Necrolemur* stands close to *Tarsius* taxonomically is most strongly suggested by essential agreement in the following areas : entocarotid relationships within the bulla ; shape and position of ectotympanic ; position of the pterygoid wings and posterior nares ; presence of a posterior palatine torus ; likeness of relative sizes of teeth, tooth patterns, and arrangement of tooth rows ; fusion of frontals, and many lesser features (Table I) which differentiate them from living and fossil lemuriform and lorisiform prosimians.

The post-cranial skeleton in necrolemurines.—Most features of the necrolemurine post-cranial skeleton reported to date need further confirmation. Schlosser (1907) assigned to *Microchoerus edwardsi* and *Necrolemur antiquus* (without association) several isolated limb-bones from the Quercy deposits. The calcanea figured by him resemble those of Primates, but there is always the possibility that the fused tibio-fibulae that he referred to *Necrolemur* actually belong to a rodent or insectivore. A fusion of this sort can occur in either order, and members of both occur in the Quercy phosphorites. The only valid association of post-cranial and cranial material in necrolemurines is reported by Weigelt (1933 : 138). His specimen includes most of the bones of a left hind limb, found together with a skull and mandibles here assigned to *Nannopithex* (p. 61). Weigelt claimed that the tibia and fibula were fused, but, on examination of the specimen, I can see no evidence for this. A small splinter of bone adjacent to the left tibia was regarded by him as a part of the fibula, but it does not contact the tibia. Also, the surface of the tibia is much worn and broken, has probably lost its original surface, and does not show any elevation for fibular attachment. Remaining parts of the pelvis and femur are not particularly like those of *Tarsius*, but the calcaneum, although broken, does show some elongation. If tibio-fibular fusion occurs in necrolemurines it has yet to be convincingly demonstrated. Moreover, it seems unlikely that the specializations of the hind limb of *Tarsius* should be expected to have been attained by any Eocene Primates. About all that can be said in defence of the possibility of such fusion is that in hopping prosimians like galagos and the tarsier the foramen magnum is directed almost downward, and since it also has this position in *Necrolemur* some such specialization of the hind limb might be expected.

Relationships.—The construction of the ectotympanic and the entocarotid circulation of *Necrolemur* are more like those of *Tarsius* than of any other known prosimian. Preservation of the bony canals of the promontory and stapedial arteries within the bulla of *Necrolemur* (Hürzeler, 1948, figs. 30, 31), shows that this form here resembles *Tarsius*, tupaioids, and Catarrhine Primates, but not lemurs or lorises (See Le Gros Clark, 1959 : 151). In consideration of the many other similarities between these two genera, it seems advisable to rank the Necrolemurinae as a subfamily of the Tarsiidae. At present the case for associating the North American Anaptomorphidae (s.s.) with *Tarsius* is not nearly as sound, and rests largely on dental resemblances between necrolemurines and anaptomorphids. Only one partial skull (of *Tetonius*) is known for any of the numerous genera and species of North

American " tarsioids ", and in it much of the basicranium is missing. Therefore, it is not particularly sound to refer to any of these New World species as tarsioids, although some of them may eventually prove to be so. At present, only the Necrolemurinae are demonstrably tarsioid.

For an early Tertiary primate *Necrolemur* is a progressive or advanced form, and in some features, such as the more complicated tooth patterns and more inflated mastoid region, less structurally primitive than *Tarsius*. Much of the overall morphology of the skull in *Necrolemur* is about as divergent from that of Eocene lemurs like *Adapis* and *Pronycticebus* as is that of the Recent tarsier. This progressiveness of necrolemurines, among Eocene prosimians, requires emphasis here because others have erroneously reported degrees of primitiveness not actually to be seen in known early Tertiary Primates, i.e. the supposed presence of three upper incisors and posterior palatine fenestrae in *Pseudoloris*. These two characters are exhibited by some Insectivora but not in Primates. Had they really occurred in *Pseudoloris* they would represent interesting morphological relics of the insectivore grade in primate ancestry, but actually *Pseudoloris* (and other necrolemurines as well) is as devoid of such features as are Recent Prosimii. In Primates antiquity is not always synonymous with primitiveness.

II. ASSIGNMENT OF *PSEUDOLORIS* TO THE NECROLEMURINAE

In 1890, Filhol described a small primate from the late Eocene phosphorites of Quercy, France, which he called *Necrolemur parvulus*. Later Stehlin (1916 : 1397) proposed a separate genus for this species, *Pseudoloris*, and pointed out a number of distinctions in the dentition separating it from *Necrolemur*. The validity of the genus *Pseudoloris* has been accepted in subsequent publications. Teilhard reviewed the species in 1921, basing his comments largely on new and more complete specimens. He disagreed with Stehlin's suggestion of an affinity between this Eocene primate and the living lorises, indicated in the generic name, and proposed that *Pseudoloris* not only had tarsioid affinities, but in some respects is more like the living *Tarsius* than any other Eocene primate. Simpson (1940 : 198) also considered the small Quercy primate particularly *Tarsius*-like and established for the one species *Pseudoloris parvulus* a separate subfamily, Pseudolorisinae, which he tentatively assigned to the Anaptomorphidae (*s.l.*) while remarking that " this genus stands considerably closer to *Tarsius* than does any other known from the Paleocene or Eocene, and should perhaps be placed definitely in the Tarsiidae ". Simpson, however, did not list any characteristics of the subfamily. In the course of recent studies on European Eocene Primates the writer has concluded that it is not possible to place *Nannopithex* and *Pseudoloris* in separate subfamilies. Since the former is clearly associated with *Necrolemur* in dental and cranial morphology and, through *Necrolemur*, with *Microchoerus*, it is advisable to formalize this association of four genera at the subfamily level. This subfamily has most often been called Necrolemurinae but the term Microchoerinae is also available. Due to greater currency and early establishment the former name is to be preferred.

Discussion.—Simpson did not specify why *Pseudoloris* should not be included in the Necrolemurinae, Teilhard having previously pointed out that among European

Primates, its closest resemblances are to species of *Necrolemur*. However, Simpson (1940 : 199, footnote) observed that *Necrolemur* may have been derived from a paromomyine, and *Pseudoloris* from an omomyine source, and so indicated a separation in their lineages going back to the Paleocene. It is unlikely that *Necrolemur* could be derived from a paromomyine stem, because the anterior lower dentition is less reduced in number of teeth than in paromomyines (unless one assumes that the anterior enlarged tooth in *Necrolemur* is an incisor, see page 58). Even assuming that the teeth in question in *Necrolemur* are incisors, then the corresponding teeth in *Pseudoloris* are also most likely to be the same. In this regard these two genera stand together in the way in which they differ from, or, as is less probable, resemble the paromomyines.

In a point for point comparison of tooth shape and pattern in *Microchoerus*, *Necrolemur*, *Pseudoloris* and *Tarsius* it is evident that there is a greater similarity between species of the latter two groups, but this agreement may equally well be due to a relative lack of specialization in tooth patterns of both, as to a phyletic connection between them not involving the other genera.

Hürzeler's illustration (1948, fig. 4) shows that *Nannopithex* (at least in the characters of premolars and molars) approaches the dentition of *Tarsius* almost as closely as does that of *Pseudoloris*. Moreover, *Nannopithex* is certainly nearly related to *Necrolemur*, so that the Tarsiinae are linked by two separate types of intermediate dental morphologies with the Necrolemurinae.

That *Pseudoloris* has one or more small incisors anterior to the large lower tooth, here considered the canine (and thereby differed from other necrolemurines) has been repeated in the literature on this primate, for instance by Hill (1955 : 313). Nevertheless, no teeth or alveoli have ever been observed in this position. The erroneous view that *Pseudoloris* possessed lower incisors seems to derive from Teilhard (1921 : 6). However, in spite of suggesting that three upper incisors indicate the existence of lower incisors, Teilhard's final statement was neutral, being only (?) for lower incisors in the dental formula he gave. Specimens of *Pseudoloris* now in the Basel and Paris collections indicate that the alveolar border of the mandible (between the large anterior lower tooth and the symphyseal surface) is too thin to have supported a more anterior tooth. Moreover, this narrow band of bone never contains evidence of alveoli.

The partial facial region of *Pseudoloris* (Montauban C) from which Teilhard concluded that there are three upper incisors in this small primate, and the only specimen of the species which preserves alveoli here indicates that the existence of an I^1 should be strongly questioned. Considering the highly eroded surface of the premaxilla the tiny spot, visible only on the right side, which Teilhard interpreted as the alveolus of an I^1 could equally well be the result of post-mortem damage. For instance, erosion of the original alveolar margin may have exposed a matrix filled cavity in the bone. If an I^1 does exist in *Pseudoloris* it constitutes a more primitive condition than occurs elsewhere among all Primates, with the possible exception of *Nannopithex raabi* in which the evidence on this point is equivocal. Furthermore, if the presence of upper incisors calls for lower ones as well, then this assumption (to mention just a few cases) would apply equally to species of *Micro-*

choerus, *Nannopithex*, and *Necrolemur*. Although the latter have two pairs of incisors above, most of the included species in these genera do not have teeth anterior to the enlarged lower tooth. The retention of P_1 in necrolemurines although P^1 is lost need not be anomalous because (unlike most Primates) members of this subfamily have rather small upper canines, which do not necessitate the formation of a diastema below for their reception. *Microchoerus ornatus* and *Pseudoloris parvulus* are at opposite extremes in this subfamily as regards dental patterns, but they are linked by a series of morphologically (not sequentially) intermediate species. If, as some authors have preferred, these genera are divided into three subfamilies, Microchoerinae–Necrolemurinae–Pseudolorisinae, the number of subfamilies approximates to the number of genera involved and completely conceals their essential similarities.

The proliferation of dental cuspules and crenulations observed in the late Eocene species of *Necrolemur* and *Microchoerus*, but lacking in *Necrolemur zitteli*, and the species of *Nannopithex* and *Pseudoloris* should not be given too much taxonomic weight. Complex molar patterns in *Microchoerus erinaceus* and *M. ornatus* particularly, were considered by some early authors as indicative of a separate subfamily or even family for *Microchoerus*. Nevertheless, such changes might be due to the spread of very few or even single gene alleles which, as the temporal succession of species in the European Eocene suggests, might have appeared and been selected for rapidly. Apart from this, necrolemurine species, including *Pseudoloris parvulus*, are so similar in general conformation of details of tooth structure, dental formula, shape of the horzontal ramus, jaw angle, depth of the mandible, and position of the primary mental foramen, that it is hard to avoid the conclusion that they belong to a distinct taxon of closely related species and genera.

Teilhard (1921) described and figured two large reniform fenestrae in the posterior palatal region of *Pseudoloris*. Such fenestrations do not occur in *Tarsius*, nor in other Primates, although some insectivores have openings here. However, in *Necrolemur* there is often an area just in front of the posterior palatine foramina where the palate is broken away. *Tarsius* also has a thin posterior palate, and in a much smaller and more delicate primate like *Pseudoloris* the probability that this part of the palatine should have been lost during fossilization or subsequent preparation is appreciable. Microscopic examination of the edges of these fenestrae shows no smooth margin but everywhere the rim of these holes is fractured and broken. Evidently these openings are not natural features but artifacts of preparation. They can no longer be considered significant diagnostic features of the genus.

Agreements between facial regions of the skull of *Pseudoloris* (Montauban C), of *Microchoerus* (Sedgwick Museum, Cambridge), and the more complete skulls of *Nannopithex* (G.P.I.H. 4236) and of *Necrolemur* include the following relatively diagnostic tarsioid features : 1) comparatively large, anteriorly directed orbits ; 2) reduction of snout size and length ; 3) narrowing of the interorbital septum ; 4) convergence of the tooth rows anteriorly ; and in the latter two genera, at least, 5) fusion of frontals in the mid-line. These shared cranial features corroborate dental resemblances discussed on page 61.

To conclude, the similarities between *Pseudoloris* and remaining necrolemurines are so great that it should be assigned to this subfamily. It may be noted that at one time or another one or more species of all the genera here included in the Necrolemurinae (*Necrolemur, Microchoerus, Nannopithex, Pseudoloris*) have been assigned to the genus *Necrolemur*.

III. THE ANTERIOR TEETH OF *MICROCHOERUS* AND *TARSIUS*

Interpretation of dental formulae in Primates.—For two principal reasons identification of the number and the kind of teeth in early Tertiary Primates is of basic importance in reconstructing primate evolutionary history. First, teeth are the most commonly preserved parts of these animals, and, second, once a tooth is lost from the series it cannot be reproduced again as such. From this latter it follows that species postulated to lie on or near the line of ancestry of a given form must have the same or a greater number of each kind of tooth than does a supposed descendant. An example is provided by the Paleocene and Eocene *Plesiadapis*. Latest known species of this genus have lost canines, first and second premolars (above and below) and a pair of lower incisors,—eight teeth in all. Since all living Primates, with the exception of the Madagascan Aye-Aye, *Daubentonia*, possess at least some of these teeth, *Plesiadapis* is thus eliminated from the near vicinity of any of their ancestral lines (and from that of *Daubentonia* on other, and very convincing, grounds ; Simpson 1935). Huxley (1876) termed such forms (which cannot have given rise to later stages of a given group) *intercalary* types. From these, he distinguished *linear* forms, which in their structure admit of the possibility of being ancestral to subsequent groups, even when the lack of intermediate connecting links makes absolute demonstration of such ancestor-descendant relationships impossible (Le Gros Clark, 1959 : 48). Although Huxley's terms have not received general acceptance they serve to emphasize the essential problem to be considered here,—whether the dental conformation in necrolemurines and tarsiines indicate *intercalary* or *linear* relationships between the two subfamilies.

A number of procedures, derived from comparative studies of all known forms govern the identification of teeth in Primates. Upper incisors in Primates, as in all mammals are always situated in the premaxilla. The upper canine, unless lost, is the most anterior maxillary tooth. When present, the lower canine is situated in front of the upper and shears against its anterior margin. Thus, the lower caniniform tooth in lemurs and lorises can be determined as the P_2 (despite a canine-like appearance), since its anterior edge shears against the posterior face of the upper canine. In these Prosimii the true canine has become incisiform and inclined forward, forming part of the tooth-comb apparatus. Apparently P_2 cannot shift forward so as to shear against the anterior face or blade of the upper canine and this makes it possible to distinguish P_2 from the canine in all cases. Identification of the anterior enlarged lower tooth in necrolemurines is not so simple, and the different assignments given this tooth have complicated discussion of possible relationships between the anterior lower teeth of necrolemurines and tarsiines.

For many years there have existed two conflicting interpretations of lower dental formula in Necrolemurinae, one affirmed by Stehlin (1916) for *Necrolemur* 0.1.4.3., favoured by Hürzeler (1948) and by Hill (1955) and another presented by

Gregory (1915), 1.1.3.3., and avowed by Simpson (1937, and later). What has been obscured by this difference of opinion is that necrolemurines typically lack a tooth in front of the enlarged tooth and behind it have seven teeth. Consequently, no matter which of the alternative dental formulae is correct, all but one species of necrolemurines differ from, or resemble, *Tarsius* in the same way. This is not reflected by the taxonomic key for the group presented by Hill (1955 : 292) in which the procumbent anterior tooth is regarded as a canine in *Necrolemur* and *Nannopithex* and as an incisor in *Microchoerus*.

Differences between anterior lower dental formulae in necrolemurines and *Tarsius* require elucidation in view of the cranial resemblance of both subfamilies. Moreover, the upper dental formulae of all species of both groups are apparently the same (2.1.3.3.), as are the sizes of the teeth relative to each other (which may be more important). For example, all tarsiids have an I^2 that is larger and longer than the upper canine.[1] This is the reverse of the condition in all notharctines, adapines, living lemurs and lorises, in which the upper canine is much larger and longer than I^2. A definite assignment as to type of the anterior tooth in the lower dental series of necrolemurines remains difficult. If it is unlikely, as Simpson (1937 : 146) remarked, that a lower canine can occlude in the position it does here, then it would appear that the lower enlarged tooth in all these European Eocene tarsioids, including *Pseudoloris*, is an incisor and that the lower canine is the reduced and premolariform tooth immediately behind it. Alternatively, the canine may be supposed to have been lost and four lower premolars retained. The presence of a small P_1 consistently in *Teilhardina*, situated somewhat to the outside of the midline of the tooth row (as in Necrolemurinae) seems significant here (in view of the other dental resemblances between *Teilhardina* and necrolemurines noted by Hürzeler, 1948). In *Teilhardina* the lower dental formula is 2.1.4.3. Because of this, it is no longer possible to say that there are no known tarsioids of the early Tertiary which retain four premolars (Simpson 1937 : 146). As Hürzeler noted the Necrolemurinae, on the basis of dental evidence, probably derive from an Old World omomyid like *Teilhardina* and represent a phylum in which progressive reduction of the lower incisors took place.

The criticism can be made that the assumption of total loss of lower incisors in typical necrolemurines has no known parallel among other Primates. This is correct, but the loss of all but a single lower pair of incisors is more common in Primates than has been previously stressed. Apart from *Tarsius* and one species of *Microchoerus* this condition also obtains in *Parapithecus*, in the adapine genera *Caenopithecus* and *Protoadapis*, perhaps in the notharctine *Pelycodus*, and in indrisines including *Indri* and *Propithecus*. Such rather broad distribution of lower incisor reduction among both living and fossil tarsioids and lemuroids indicates that parallelistic tendencies for tooth loss here are strong among Primates, and make the total loss of lower incisors in late necrolemurines appear more plausable than the assumption that the large lower anterior tooth is not a canine but an incisor, as in plesiadapids and *Phenacolemur*.

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[1] The most anterior upper incisor in necrolemurines is here arbitrarily considered I^2.

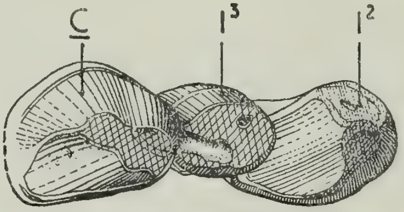
Should the enlarged anterior tooth be an incisor in Necrolemurinae then all members of this group stand distinctly apart from *Tarsius*, and it could not have descended from a species even distantly resembling necrolemurines in this regard. However, an alternative interpretation is suggested by specimens of *Microchoerus erinaceus* and *M. edwardsi* in the British Museum (Natural History) which is much more in agreement with the tarsier dental formula.

The British Museum specimens.—The lower dental formula of *Tarsius* is generally assumed to be 1.1.3.3. From front to back in the mandible these teeth are identified as, first, a small, pointed incisor, followed by a large and long canine, three premolars (increasing in size posteriorly), and three simply constructed molars, of which M_2 is the largest. In necrolemurines, on the other hand, the lower dental formula (assuming the anterior tooth is a C) is written 0.1.4.3. However, an exception to this formula apparently occurs in one necrolemurine species. Two specimens of *Microchoerus edwardsi* in the British Museum show a small alveolus anterior to the enlarged procumbent tooth, giving a lower dental formula of 1.1.4.3. This is further confirmed by a specimen of the same species in the Paris Museum (identified as Bach, lot 1893–11). Other necrolemurines do not show this small anterior alveolus. However such a possible identification of the lower dental formula of *Microchoerus edwardsi* (because that of *Tarsius* could be derived from it) indicates the need for a more certain assignment of the large procumbent lower tooth in necrolemurines. Some clarification of this point is provided by the following specimen of *Microchoerus* in the British Museum (Natural History).

The holotype of *Microchoerus erinaceus* Wood, B.M.N.H. 25229 (Text-fig. 2) includes the entire upper dentition (on one side or the other) and an associated mandible with P_3–M_3. The anterior half of this jaw (with all teeth) was part of the original find, by Wood (1846). Cooper (1910) noted that the anterior portion of this mandible had been lost. However, the series of specimens of *Microchoerus erinaceus* in the British Museum (Natural History) from the late Eocene deposits near Hordle, Hampshire and from various localities in the Isle of Wight is extensive and includes several isolated lower canines, and a number of anterior parts of mandibles with premolars. These specimens of *Microchoerus erinaceus* are also supplemented by a number of jaws and a fragmentary facial region from Hordle in the Sedgwick Museum, Cambridge. The occlusal diagram shown here (Text–fig. 2) is based on the holotype, supplemented by the others mentioned above and by Wood's figure.

The holotype has well-preserved wear facets on the three anterior upper teeth, I^2, I^3, and *C*. These surfaces of wear indicate that the tip of the lower canine could be extended anteriorly to occlude against I^2, presumably when the animal was nibbling, but that when the jaws were shut its apex wore against I^3 and its base against the upper canine (see Text fig 13b). In *Tarsius*, the lower canine (which no one seems to doubt is a canine) can likewise occlude against these same three upper teeth. In *Tarsius* there is not the same degree of procumbency as in *Microchoerus*, so that wear on these three upper teeth in the living species, takes a rather different course. However, relative sizes of the teeth involved, and their general position in the jaw is similar in both genera, and upper dental formulae the same.

FIG. 2A Upper right I^2–$\underline{C}$:



$\underline{C}$–I^3: Cross hatched–wear surface sloping postero-lingually made by lower canine when teeth are fully occluded.

I^2: Cross hatched (fine) internal wear surface made by lower canine when nibbling

I^2 Dotted lines–external wear surface made when lower canines are swung laterally during nibbling.

FIG. 2B Left anterior dentition (fully occluded).

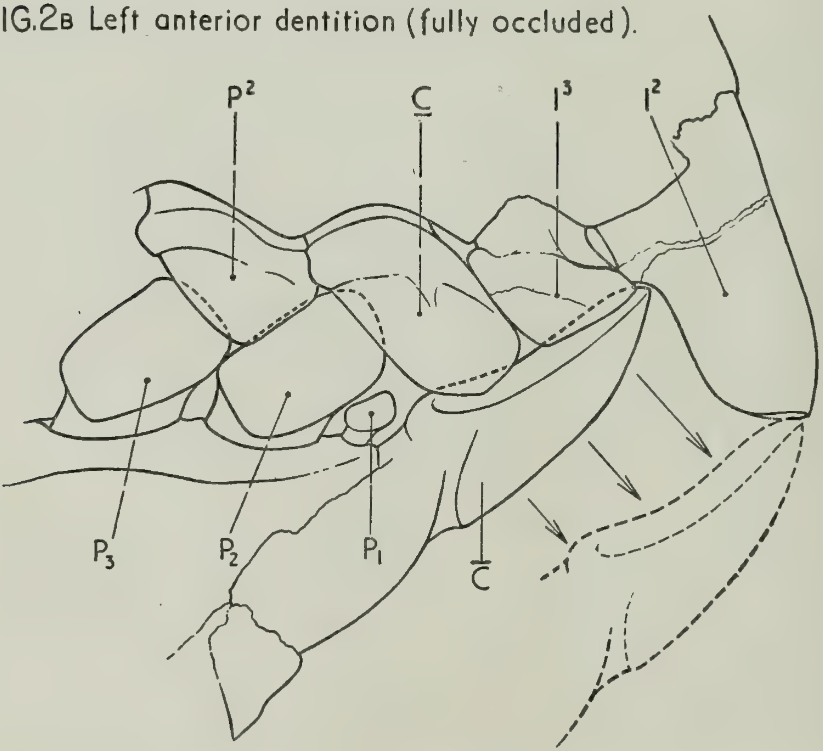


FIG. 2. *Microchoerus erinaceus* Wood. Diagrams of anterior wear pattern and occlusal relationships. (B.M.N.H. 25229).

A reasonable assumption would be that a generalized necrolemurine, with a lower dental formula identical to that of *Microchoerus edwardsi* could have given rise to that of *Tarsius*.[1] All that would be needed to achieve this is loss of P_1 (already non-functional in necrolemurines) and reduction of the degree of procumbency of the anterior lower teeth. If, in spite of the foregoing analysis, anyone still prefers the idea that the enlarged anterior tooth below (in this subfamily) is an incisor, then it would be equally logical to conclude that the large second tooth in the lower dentition of *Tarsius* is also an incisor. It is known that the P_2 in Primates can become caniniform, but apparently no one has yet suggested that incisors might do this also.

One reservation regarding lower dental formulae in this group should be made. Because of the great delicacy of the anterior alveolar border of the mandibles in these small mammals, and consequent breakage, it is difficult to be certain that they could not have had teeth anterior to the lower canine. Nevertheless, I have not found alveoli in this position except in *Microchoerus edwardsi*. Dental formulae in remaining necrolemurines may be written as follows :—

Microchoerus erinaceus $\frac{2.1.3.3.}{0.1.4.3.}$	*Pseudoloris parvulus* $\frac{2.1.3.3.}{0.1.4.3.}$
Necrolemur antiquus $\frac{2.1.3.3.}{0.1.4.3.}$	*Nannopithex raabi* $\frac{2.1.3.\ (\text{or } 4).\ 3.}{0.1.4.\qquad 3.}$

As will be seen from the above formulae it is fairly certain that all four species have the same number and kind of teeth, identical with the living *Tarsius* above, but differing from the latter in lacking the single pair of lower incisors, and in possessing a vestigial P_1.

IV. REVISION OF *NANNOPITHEX* AND ITS RELATIONSHIP TO OTHER NECROLEMURINES

Taxonomic position. An examination of the type of " *Psuedoloris abderhaldini* " Weigelt (1933) indicates conclusively that it is conspecific with " *Necrolemur* " *raabi* Heller (1930). The later species is referable to *Nannopithex*. Weigelt was perplexed by the recovery of a skull different from *Necrolemur* (G.P.I.H. 4236) associated with lower jaws that were remarkably like those of "*Necrolemur*" *raabi*. These mandibles were illustrated by Weigelt (1933, pl. 4, figs. 2A, B), who quite correctly observed that this upper dentition could not belong to a species of *Necrolemur*. He therefore described the specimen as a new species of *Pseudoloris*. This assignment, although still not correct, was an improvement. In the vicinity of this specimen were also collected elements of a left hind limb of a primate. These Weigelt believed could be assigned with high probability to the same individual as the skull (G.P.I.H. 4236). As such, they comprise the oldest partial skeleton of a tarsioid.

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[1] *Microchoerus edwardsi* appears to be disqualified as a direct forerunner of the tarsiers by possession of complexities in cheek tooth patterns not seen in *Tarsius*.

Published observations on the Geiseltal species of *Nannopithex* are somewhat confusing because of the early misidentification of the generic position of the Brown Coal species and it is necessary to outline the successive views held regarding it and closely allied forms. Simpson (1940 : 199) questioned the taxonomic placement of the " two " species and first suggested that evidence for a specific separation of " *Pseudoloris abderhaldini* " and " *Necrolemur* " *raabi* is dubious.

In an attempt to separate the two supposed species, Weigelt went to great lengths to set out some consistent differences in their mandibular dentitions. These distinctions are not convincing. It appears that the individuals called " *Necrolemur* " *raabi* are in most respects slightly larger and have a deeper horizontal ramus of the mandible than has " *Pseudoloris abderhaldini* ". There does not seem to be any distinction between the two " types " that could not be due to sexual dimorphism or to population variation within one species. The partial skeleton of " *Pseudoloris abderhaldini* " was recovered from the Leonhardt Mine locality, while all the individuals of " *Necrolemur* " *raabi* appear to be from the Cecilie Mine. It is unlikely that the fossil-bearing strata in the two mines are of exactly the same age, but no appreciable time interval can be assumed.

Not knowing the upper dentition, Heller (1930) had some basis for placing " *Necrolemur* " *raabi* in the genus *Necrolemur*, even though later evidence proves this determination to be wrong. His assignment was plausible at that time because of the strong similarity in lower tooth structure between the German form and some of the less specialized necrolemurines such as " *Necrolemur* " *filholi*. In defence of Weigelt's placement of the species he described, it can be said that the upper dentition of " *Pseudoloris abderhaldini* " is superficially like that of *Pseudoloris parvulus*. This is mainly because, in dental patterns, they are both of a rather generalized tarsioid type. However, this similarity is not profound, and the lower dentitions of the two species are quite different.

Hürzeler (1948) tentatively equates *Necrolemur filholi* Chantre & Gaillard (1897) with *Nannopithex pollicaris* Stehlin (1912). He appears to hesitate somewhat on the question of whether or not to retain the genus *Nannopithex* for this form, but the identity of the two species seems to be beyond question. Although *Nannopithex filholi* has much simpler cusp patterns than *Necrolemur antiquus* the two are linked morphologically by *Necrolemur zitteli*, as is convincingly demonstrated by Hürzeler (1948).

Hürzeler's elucidation of the dental characters of *Nannopithex filholi* has provided the key to the correct assignment of the Brown Coal necrolemurine. Comparisons of the two species indicate that they are congeneric. The evidence (given below) for a specific distinction between them is not extensive, but at present it seems better to retain *raabi* for the Geiselthal form. Both species of *Nannopithex* appear to be of early Middle Eocene age. Faunal correlations indicate that species of this genus occur in Lower or Middle Lutetian deposits. At present, specimens of *Nannopithex* have been recovered near Egerkingen in Switzerland, at Buchsweiler in Alsace, and in the Geisel valley near Halle, Germany. *Nannopithex* does not occur in the Quercy phosphorites of Bartonian and Ludian age. Its absence at this later period reinforces the idea based on morphology that a species of this genus could have given rise to *Necrolemur*.

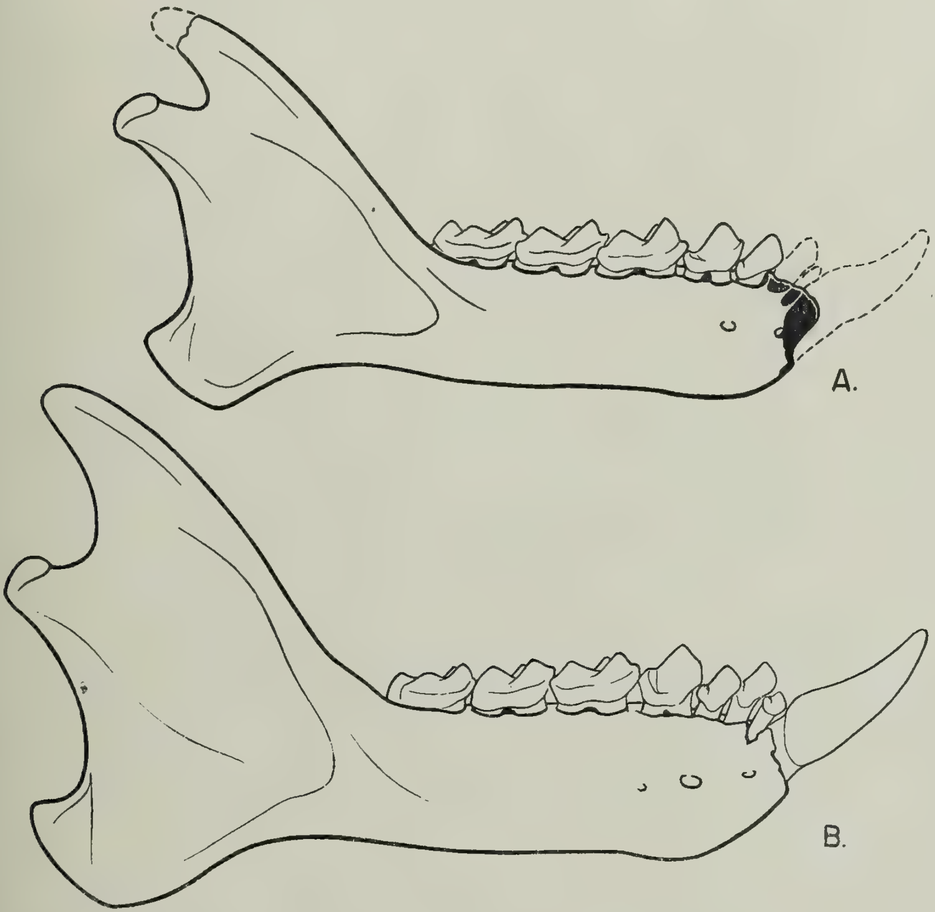

Fig. 3. A. *Pseudoloris parvulus*, based onmandibles in the Paris Museum, × 8 approx.

B. *Nannopithex raabi*, based on specimens at the Geological and Paleontological Institute of Halle University, particularly G.P.I.H. 4254 and 4255 × 8 approx.

Genus **NANNOPITHEX** Stehlin, 1916

Type Species.—*Nannopithex policaris* Stehlin, (=*Necrolemur filholi* Chantre & Gaillard).

Generic characters.—$\frac{2.1.3.\ (\text{or } 4).\ 3.}{0.1.\qquad 4\ .\ 3.}$—Upper M differs from that of *Pseudoloris* in presence of nannopithex-fold running from posterior crest of protocone toward hypocone. Hypocone of M^1 comparatively smaller than in *Pseudoloris* ; external median indentation between paracone and metacone of M^{1-3} less pronounced, and metacones of M^{1-3} relatively smaller and lower than in *Pseudoloris* ; all teeth with some crenulation of enamel suggestive of teeth of *Necrolemur* but unlike those of *Pseudoloris*. P_4, compared to lower molars, much larger, and molar cusps more rounded and less high than in *Pseudoloris* ; molar paraconids more distinct than in *Pseudoloris* ; M_3 entoconid and hypoconulid not as high or as sharply set off as in *Pseudoloris*. (Known species slightly smaller than *Tarsius spectrum* or *Necrolemur zitteli*, somewhat larger than *Pseudoloris parvulus*.)

Discussion.—Considering that *Pseudoloris* and *Nannopithex* possess very simple and unspecialized dental patterns the differences between them are marked, being about as great as those which separate either from the living *Tarsius*. However, both show distinct affinities with *Necrolemur* and with *Microchoerus* as well as with *Tarsius*. Insofar as dental characters go (and osteological features do not contradict them) no basis whatever remains for placing these five genera in several different families and sub-families, as has been done in the past.

The skull of *Nannopithex raabi* from Halle retains the entire upper dental series on one side or the other (except the canines) and this indicates the dental formula given above. Weigelt (1933 : 129) suggested an upper dental formula of 2.?.3.3. for the Geiseltal species, but his discussion, figures, and (much better) the specimen itself, indicate another possibility, 2.1.4.3., (Weigelt, 1933, pl. 5, figs. 1, 4, 5) for the upper dentition of *Nannopithex raabi* (G.P.I.H. 4236). This photograph shows that the most anterior tooth preserved in position is much smaller than that just posterior to it which is clearly P^2. Although there is some breakage in the specimen, microscopic examination confirms that the seven teeth of the upper left side are an unbroken series. The four anterior teeth make up a sequence increasing in size posteriorly, and (considering what is known of the anterior upper teeth in *Microchoerus* and *Necrolemur*, and of these teeth in European Eocene Primates generally) they can hardly be other than the series P^{1-4}. Such an assumption is particularly necessary, if, as Hürzeler has suggested, a species of *Nannopithex* is to be considered ancestral to *Necrolemur antiquus*. Otherwise, it is required to assume that in the line leading through *Nannopithex* to *Necrolemur* the upper canine was first reduced (from a primitive large size, presumed characteristic of ancestral Primates) to a size smaller than the P^2 and subsequent to this re-acquired a size larger than that which the P^2 has in *Pseudoloris*, *Microchoerus* and (as is more important) in *Necrolemur*. It is more likely, therefore, that the canines have been lost from this specimen. Weigelt is apparently correct in his identification of the two loose teeth found in the region of the anterior extremity of this skull. The larger and most anterior tooth he considered I^2, a smaller one I^3. These teeth resemble I^{2-3} of *Microchoerus*. Should the dental series be complete in G.P.I.H. 4236 then the smaller tooth anterior to the P^2 would have to be considered a canine, and the D. F. would be 2.1.3.3. above, as in *Microchoerus* and *Necrolemur*. Even so, this is a different formula from that given by Weigelt which is one tooth short by his own account. The presence of a small upper P^1 would correlate well with the dental formula expected for a necrolemurine ancestor.

NANNOPITHEX RAABI (Heller)

(Text–figure 3)

1930. *Necrolemur raabi* Heller, p. 35, pl. 5, figs. 5, 6.

1933. *Pseudoloris abderhaldini* Weigelt, p. 128, pl. 3, fig. 5 ; pl. 4, figs. 1–3 ; pl. 5, figs. 1–5 ; pl. 9, figs. 4, 5 ; text-figs. 1–3.

MATERIAL.—G.P.I.H. 4254–4257, mandibles, and G.P.I.H. 4236, skull, with associated mandibles and hind limb.

HORIZON AND LOCALITY.—Gesieltal Brown Coals, Middle Eocene ; near Halle am Saale, Germany,—from Leonhardt and Cecilie mines.

DIAGNOSIS.—Size : about as in *Nannopithex filholi* or slightly larger. Protocones of P^{3-4} somewhat more distinctly set off than in *Nannopithex filholi*, P^2 slightly longer antero-posteriorly than in the latter species ; nannopithex-fold on M^2 less distinct than in *Nannopithex filholi*. Mandible : M^3 hypoconulid slightly more distinct than in most specimens of *Nannopithex filholi* but enamel crenulations not as pronounced as in latter.

Discussion.—The lower teeth of *Nannopithex raabi* approach more closely the dentition of *Nannopithex filholi* from Buchsweiler, in Alsace at Basel, Bchs. 647, than they do the specimen from Egerkingen, Basel Eh. 601,—particularly in the conformation of the M_3 talonid. Otherwise, except for the characters mentioned in the diagnosis above, the dentitions of the various specimens of *Nannopithex* illustrated by Hürzeler (1948) are not very distinct from the Geiseltal specimens. Pending a better understanding of faunal correlations and, as long as so few really complete individuals are known, it seems better to retain two species for the genus *Nannopithex*.

Perhaps the greatest significance of the Geiseltal finds of *Nannopithex* is the information supplied regarding early primate anatomy by the comparatively complete skull, mandibles, and hind limb found there. These remains make up the oldest known partial skeleton of an Old World primate. As a consequence of their significance, these remains were discussed in some detail by Weigelt, and will not be repeated here. There are, however, a few further comments of value to be made about the specimen.

Although the skull is crushed, it is evident that the orbits in this primate were very large. Most of the posterior wall of the orbit can be seen on the left side and it stretches from the lateral extremity of the skull to the mid-line (Weigelt, 1933, pl. 3, fig. 1). On the left side of the dorsal surface of the frontal the supraorbital margin and the juncture with the zygomatic arch is preserved. This region is very similar in appearance to the corresponding area of *Necrolemur* skulls and, as in the latter, the interfrontal suture appears to be closed. Most of the characters of the basicranium are indeterminate, but in the region of the left external auditory meatus are numerous fragments of cancellous bone, which are presumably remnants of air cells of an inflated mastoid region, as in *Necrolemur*. The appearance of the detached back of the palate also agrees with that of *Necrolemur antiquus*.

As already mentioned (p. 53) the hind limb figured by Weigelt provides no evidence that this primate had distal fusion of tibia and fibula, which is commonly supposed to be the case in Necrolemurinae. Simpson (1940 : 196) expressed the opinion that there is a general resemblance between the hind limb of the Geiseltal tarsioid and that of *Hemiacodon*, insofar as he was able to determine without seeing the originals. Examination indicates that, as he then suggested, most of the features of difference from *Hemiacodon* apparent in the Halle specimen seem to be the result of crushing.

MEASUREMENTS (in. mm.) *NANNOPITHEX RAABI*

(Specimens at the Geological and Paleontological Institute of the Martin-Luther University of Halle-Wittenberg, Halle-am-Saale, Germany). G.P.I.H. 4236, Leonhardt Mine, holotype of " *Pseudoloris abderhaldini* ".

Maxilla :	Anteroposterior diameter	Transverse diameter
P^1	1·1	0·7
P^2	1·8	1·1
P^3	1·7	2·0
P^4	1·5	2·3
M^1	1·9	2·5
M^2	1·8	2·7
M^3	1·4	2·2

Anteroposterior diameter p^1 through M^3,—10·1 mm. G.P.I.H. 4255, Cecilie Mine. Mandible :—

Anteroposterior diameter $\bar{C}$ through M_3,—11·7 mm.
Anteroposterior diameter $\bar{C}$ through P_4,—6·8 mm.
Anteroposterior diameter M_1 through M_3,—4·9 mm.

NANNOPITHEX FILHOLI (Chantre & Gaillard)

Discussion.—Inasmuch as the studies undertaken by the writer are in agreement with Hürzeler's tentative equation of *Nannopithex pollicaris* and *Necrolemur filholi* this species takes the name *Nannopithex filholi*, as discussed above. Hürzeler (1948) figured and reviewed amply all known materials of this species. Consequently, it will not be re-diagnosed here. One possible difference between Stehlin's type species and the mandibles described by Chantre & Gaillard is that the P_4 of the former specimen does not have the roots as well separated as in typical *Nannopithex*. However, this character is variable in individual specimens of *Necrolemur*, and may not have much taxonomic value.

V. CONCLUSIONS

The findings reported here substantiate the position that tarsioids can be distinguished from lemuroids as far back as the Middle Eocene. Neither the Middle Eocene *Nannopithex*, nor the better-known genus *Necrolemur* provide any anatomical basis for a horizontal grouping of the Necrolemurinae with contemporary Eocene lemuroid Primates. Consequently, the Necrolemurinae have been ranked under the Tarsiidae.

Tarsioid claims for any other early Tertiary primate stocks are hard to support on the basis of present evidence. Some or all of the forms now ranked in the Omomyidae and Anaptomorphidae, may eventually prove to be so (with the advent of new and better specimens), but demonstrating tarsioid characters—ultimately derived from the living genus—becomes increasingly difficult with greater antiquity. Because of this it is possible that the direct ancestry of the Necrolemurinae might not have been definable as tarsioids much before the early Eocene.

Probably *Teilhardina*, an *Omomys*-like primate from the Belgian early Eocene (Sparnacian), bears a relationship to the stock from which the necrolemurines arose, and it in turn suggests an omomyid derivation for these tarsioids. A complex of characters including large anterior lower teeth, a tendency toward reduction of tooth number, frequent occurrence of a large $P\frac{4}{4}$ (non-molarized), nannopithex-fold and a number of other features suggests that the anaptomorphids (s.s.) are also a closely related stock. The current narrowly drawn higher categories of Paleocene and Eocene primates tend to obscure broad synthetic similarities among a number of stocks, but without better material there is little basis for grouping together any of such currently proposed early Tertiary primate families as Adapidae, Omomyidae, Anaptomorphidae, Paromomyidae (including Phenacolemurinae), and Tarsiidae (including Necrolemurinae).

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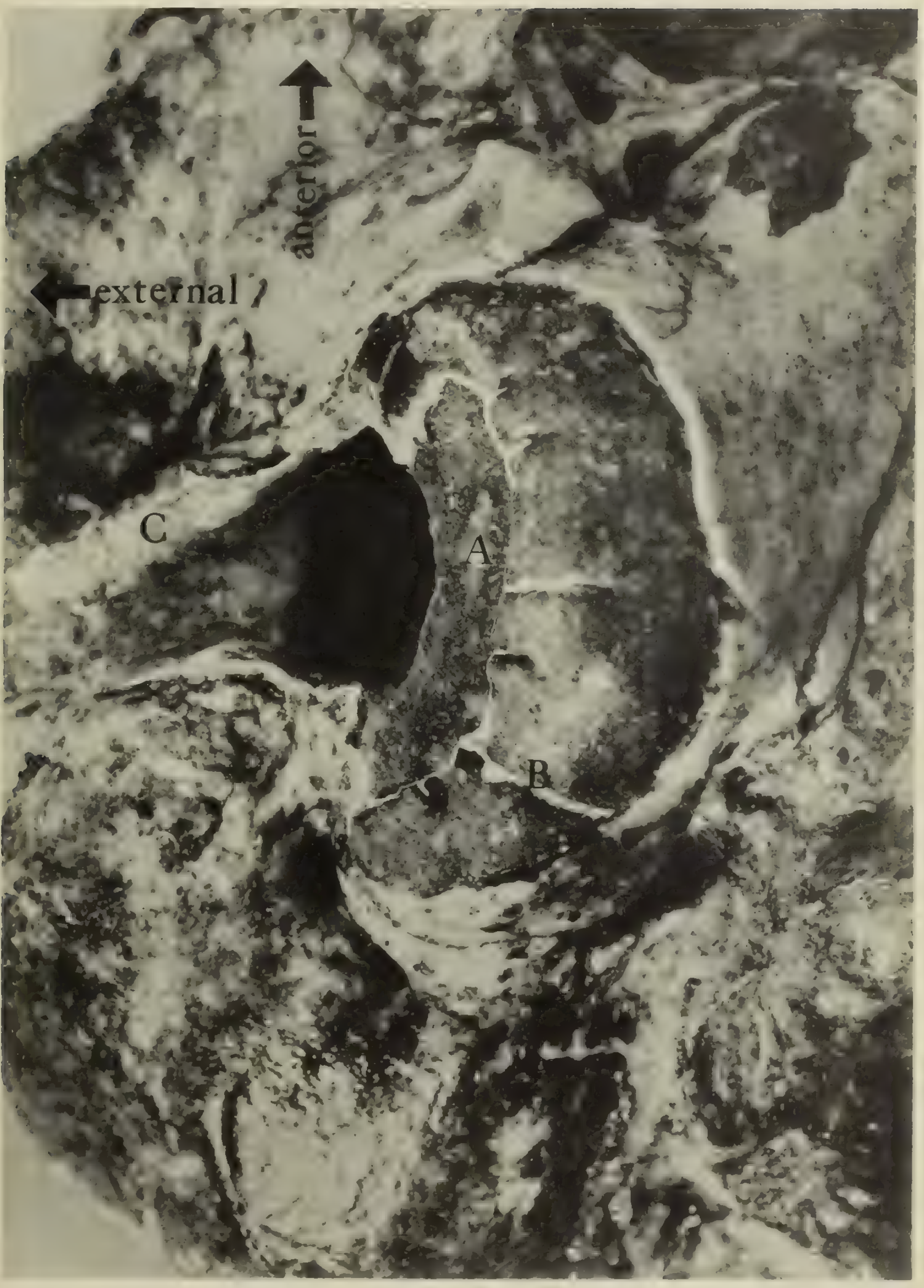
PLATE 12

Necrolemur antiquus Filhol.

Ventral view of right auditory bulla, slightly retouched. A, region of ectotympanic and ventral bulla wall. B, strut between bulla and internal margin of ectotympanic. C, part of tubular osseous meatus. × 10. (B.M.N.H. M 4490).

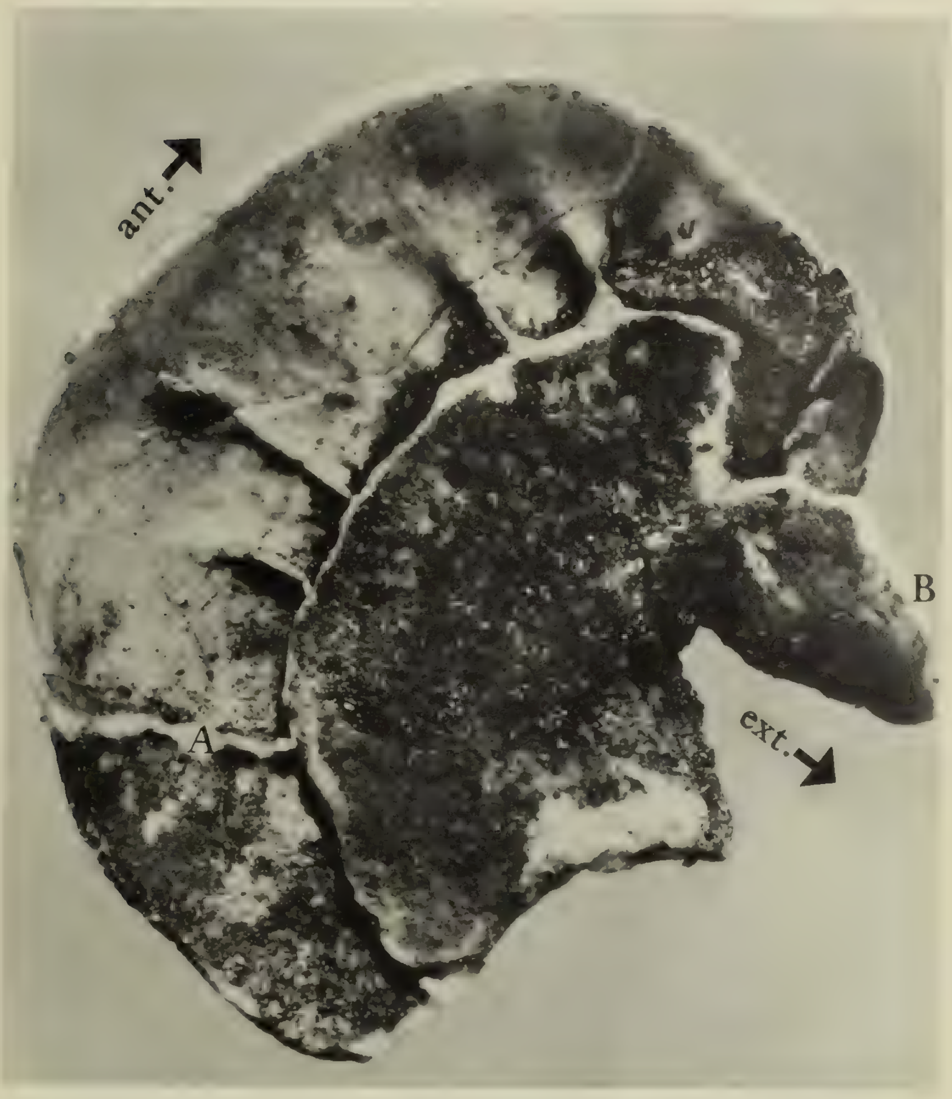

anterior
external
C
A
B

NECROLEMUR

PLATE 13

Necrolemur antiquus Filhol.

Internal view of part of the ventral wall of the right auditory bulla, showing expanded ectotympanic fused to bulla by struts (A) and continuous with broken osseous meatus at (B). × 20. (B.M.N.H. M 4490).



NECROLEMUR

PLATE 14

Adapis parisiensis Blainville.

Auditory bulla, left side (with ventral wall removed), showing free annular ectotympanic within the bulla at A. × 5 approx. (B.M.N.H. M 1345).

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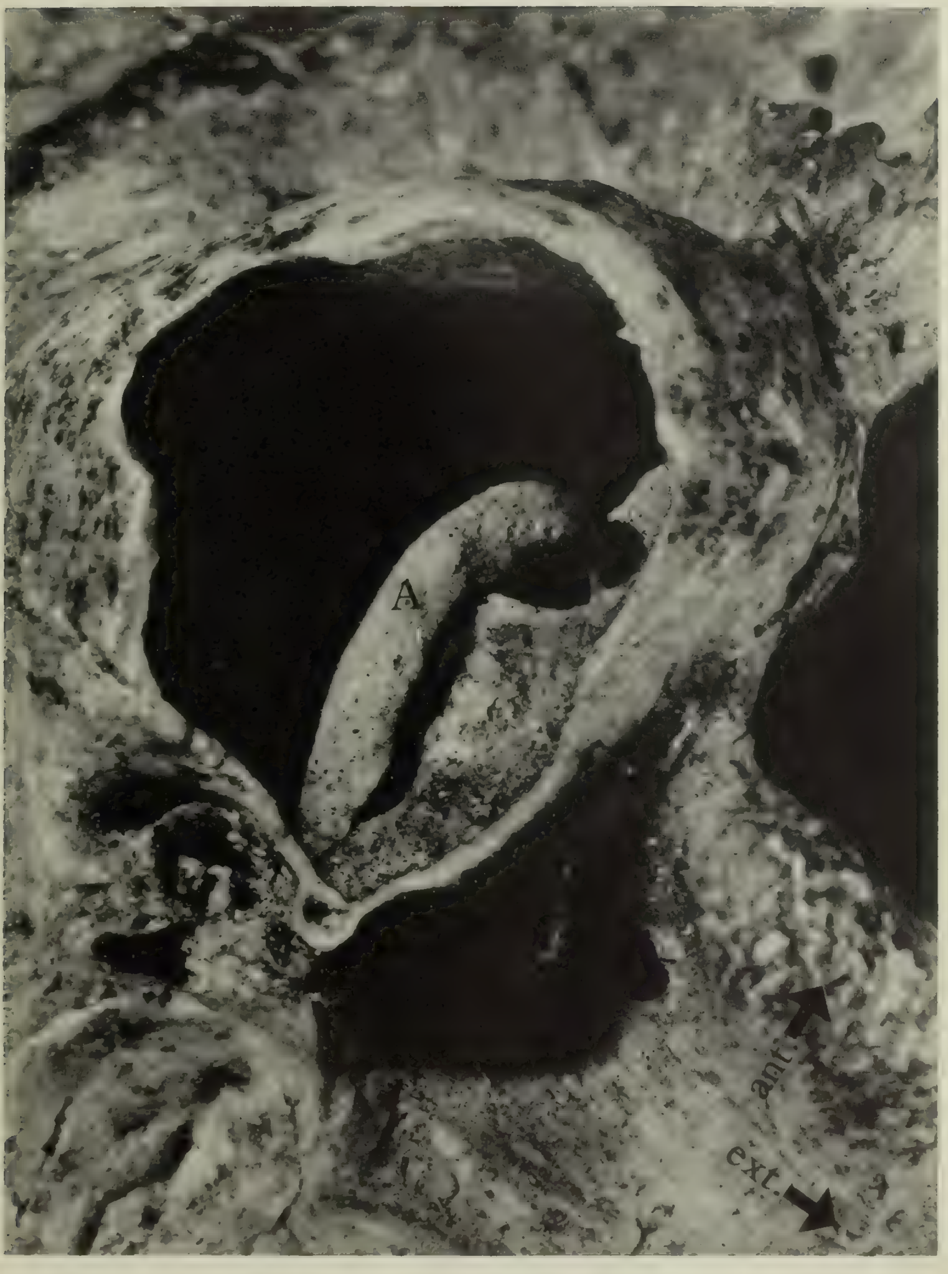

ADAPIS

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(Rhodes-Livingstone Museum)

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FRACTURED CHERT SPECIMENS FROM THE LOWER PLEISTOCENE BETHLEHEM BEDS, ISRAEL

By J. DESMOND CLARK

SYNOPSIS

This paper describes the specimens of fractured chert associated with a Lower Pleistocene fauna recovered during excavations from 1935–40 in a sink or swallow hole at the highest point of the Jordan arch. Analysis shows the cherts to have been fractured by several agencies—heat, percussion and pressure. They are compared statistically with various natural and humanly fractured collections from other areas. The criteria of artificially worked stone—striking platform, bulb of percussion and flat angle of edge-flaking—are absent from almost all the Bethlehem specimens, from which it is deduced that they owe their fractures to natural causes both before and after incorporation in the sink, though the possibility that some of them may have been *used* cannot be entirely ruled out.

INTRODUCTION

THIS paper is complementary to that by Dr. D. A. Hooijer (1958) on the mammalian fauna of Villafranchian age found in the Bethlehem Beds of Palestine during excavations between 1935 and 1937 and again in 1940.

A considerable quantity of chert was found associated with the mammalian fauna. Dr. G. Caton-Thompson had briefly examined the fractured chert specimens from this site and reported (*In* Gardner & Bate, 1937) that some of them conformed closely in shape and edge trimming to the classic Harrisonian eoliths and, therefore, suggested that some of them might be humanly fractured. In view of subsequent investigations into the differences between natural and artificial fracture of stone and into the circumstances under which nature can sometimes simulate human workmanship, a further examination of the Bethlehem stones was considered justified, to see whether the possible human origin of some of the specimens could be confirmed. Accordingly, at the invitation of Dr. K. P. Oakley, the writer made this examination and wishes to express his grateful thanks to the Trustees of the British Museum for giving him the opportunity to undertake this study and making available the excavation reports and drawings, to Dr. K. P. Oakley for his most helpful criticism and advice and for generally facilitating this study, to Miss E. W. Gardner for very kindly checking the section drawing, and to the Keeper of the Department of British and Mediaeval Antiquities, British Museum, for permission to examine the assemblage from the Kafu gravels, Uganda. My thanks are due to the Wellcome Trust for allowing me to make use of the field note-books and photographs of the Bethlehem site which was investigated as part of the work of the Wellcome Archaeological Research Expedition to the Near East, 1935–1937. Special thanks are also due to Miss Rosemary Powers for the illustrations of the Bethlehem specimens that accompany this paper.

It cannot be too strongly emphasized that assemblages of Palaeolithic implements must always be examined in relation to the nature and processes of formation of the deposit in which they are found and to the circumstances under which they have been preserved. Particularly is this important where the assemblage is suspected of dating to the very beginning of tool-making times, since the earliest tools and techniques of stone-working may be expected, by reason of their experimental " crudeness ", to simulate in varying degree naturally fractured stone. Indeed, in the beginning, naturally sharp pieces of stone and specimens worked by the earliest hominids would be likely to have been used indiscriminately and to occur together at the living sites.

The Lower Pleistocene (Villafranchian) age of the Bethlehem fauna, places the associated chert specimens near or even on the boundary line where evidence of the earliest tool-making hominids has been found. Thus it is particularly important that this assemblage should be examined as a whole in the light of present knowledge of the differences between human and natural fracture and an attempt made to distinguish between the possible agencies that brought about the fracture of these specimens.

THE SITE AND STRATIGRAPHY

The following summary of the situation and geology of the site is taken from the excavators' preliminary report (Gardner & Bate, 1937) and from the day books. Well-digging in a garden at the highest point of Bethlehem (790 metres above sea level) from where the country falls away on all sides, brought to light the first mammalian bones 15 metres below the surface in 1934. During three field seasons, in 1935–36 and 37, excavations were undertaken by Miss E. W. Gardner and the late Miss D. M. A. Bate with support from the Trustees of Sir Henry Wellcome and Sir Robert Mond. The excavation was completed by Dr. M. Stekelis in 1940, but no chert specimens from this last season's work were available for examination in London.

The fauna and fractured chert of all sizes occurred in a loose gravel set in a stiff clay matrix which was found under decomposed soil and a superficial secondary limestone. The beds dip, often steeply, to the northeast and south and it appears that they are following a funnel-shaped hole in a hard, lime-cemented chalky scree or breccia known locally as " *nari* ", containing many limestone blocks. The gravel lies against this scree deposit at a steep angle and sometimes penetrates into it as pipes, while on one side the *nari* arches over the gravel. This steeply dipping scree face was followed down for 11 metres to a small platform from where it again plunged downwards. The scree contained no fauna or fractured chert and was clearly formed under sub-aerial conditions long prior to the accumulation of the gravel. Minor constituents of the gravel were limestone blocks and pebbles, especially in places adjacent to the calcareous scree and a few iron nodules. All these materials were little sorted and were mostly derived from local Cretaceous rocks. On one side of the excavation a layer of pure clay, sterile of fauna or chert, separated the gravel into an upper and a lower half but on the opposite side this clay lenses out and it can be seen that the gravel is all of one age.

In places where some protection has been afforded to it, as, for example, on the platform mentioned above, a grey bone-bearing gravelly clay is found between the gravel and the wall of the cemented scree. It would seem that this was formed somewhat later than the main deposit of red coarse gravel.

At one place, also, a 6-metre deep pipe was found penetrating the cemented scree and filled with angular blades (*sic*) of chert of all sizes set in a red, gritty clay matrix. On the south side near the base of this pipe and caught up in pockets of red clay in the *nari* were found some highly polished and glazed chert pebbles mixed with quite unworn and angular fragments.

The gravels rapidy contract with depth. When taken in conjunction with the inward dip of the beds, this fact made the excavators conclude that the gravels formed the filling of a roughly funnel-shaped hole or sink, or alternatively that they had reached their position as a result of the collapse of the original floor on which they were laid. Sliding and slumping of the deposit in some places confirms that collapse of the floor of the sink had taken place after or during the process of gravel filling.

Included as an Appendix is a report by Dr. S. H. Shaw, then Geological Adviser to the Government of Palestine. This followed from his examination of the site during the 1940 excavations and confirms Miss Gardner's interpretation of the nature of the deposits. There is, however, some disagreement as to the importance of the part played by water in the accumulation of the gravel and clay. The deposits are clearly not waterlaid in the sense of their having been accumulated by river or stream action, yet the abrasion of most of the chert specimens is such that they are likely to have acquired this in the course of general terrestrial weathering. This weathering probably occurred while they were lying on the surface prior either to being washed by stormwater or falling into the sink while this was gradually collapsing and filling up over an appreciable period of time. The sink was formed as a result of local solution of the *nari* but the comparative rarity of limestone fragments in the gravel and clay, except in the lower levels and in the parts adjacent to the *nari*, of which they form an integral part, shows that while purely residual elements were an important contributory factor to the filling of the hole, the main part of the gravel was derived from the surface outside.

The deposit is mainly, therefore, in the nature of an eluvial accumulation such as might be expected to have resulted from intermittent and fairly rapid run-off under semi-arid rather than consistently wetter conditions. The chert shows signs of having been subjected to many mechanical forces—striation, shattering, bruising, crushing, rolling and thermal action. Generally speaking, however, the amount of typical abrasion by water rolling is very slight and a considerable proportion of the specimens are relatively fresh while a few are completely so.

It is interesting to note that the faunal remains, which occur from 1·75 metres to 15 metres down in the gravel, have not been subjected to quite the same amount of mechanical weathering, though they have been subjected to fracture by pressure indicating that some movements must have taken place since their inclusion in the deposit. Moreover, the excavators report that it seemed as if complete carcases may have been embedded in the deposit. Indeed, in Africa, as no doubt elsewhere, it is not uncommon to find whole carcases of animals that have fallen into sinks perhaps in search of water. The fauna, which contains *Archidiskodon planifrons*, *Leptobos* and *Hipparion* (Hooijer, 1958) indicates a warm climate but with a more liberal supply of permanent water than exists in the region to-day.

Dr. Hoojier's examination shows the animal remains to be all of one age and representative of a basal Pleistocene fauna, which appears to be Asiatic in origin though it provides links for this period between Asia and Africa.

Plate 17 is an attempt to reconstruct the general stratigraphy of the site based on the excavators' reports, photographs and the day books. Unfortunately the detailed section drawings were not available, but Miss Gardner has confirmed that the reconstruction is accurate so far as the main facts are concerned. Plates 15 and 16 show the general situation of the site and details of the stratigraphy.

DESCRIPTION OF THE SPECIMENS

A. *Nature of the Raw Material*

Only the chert shows any evidence of fracture. This material is found in two forms. The one is a tabular chert of varying thickness, the average being between 10 and 15 mm. with pitted or corrugated cortex. In colour it is mainly a pale, greeny brown. The other form is a nodular chert, usually black to grey in colour. Also represented, though rarely, is a brecciated chert in which yellow to cream concretions are set in a red-brown to grey matrix. Acheulian man favoured the use of this latter material at certain sites in southwest Asia.

The chert was found in all sizes—from large blocks measuring half a metre or more to small fragments only a few millimetres long—and was in the main derived from local Cretaceous rocks.

B. *Physical Condition and Patination*

By far the greater majority of specimens have been patinated and abraded by sub-aerial weathering which has rounded and bruised the aretes and edges before incorporation in the gravel. Very few pebbles or specimens in the collection show the higher degree of abrasion that results from long incorporation in a stream gravel though some pebbles (of limestone) do occur. The glossy patina seen on certain small pebbles and flaked fragments from the lower part of the deposit has already been referred to. These specimens come from pockets of red clay in the *nari* and show a very high degree of natural glazing. There are no more than two dozen of these specimens but their appearance is strikingly different from that of the remainder of the material. This type of glazing is very similar to that exhibited by tools in many Quaternary river gravels and in some spring deposits in tropical Africa where silica rocks form the chief ingredients. The glaze is generally considered to have been brought about by rapid temperature variation in an environment with a fairly high rainfall having a marked seasonal variation and results from a concentration on the surface of silica derived from the interior of the stone (Phaup, 1932).

Only a very few of the chert specimens show entirely fresh edges and lack of abrasion and from these some interesting deductions are possible. Numbers of the abraded specimens, however, show varying degrees of localized fresh fracture, and this differential abrasion is one of the most significant features of the collection. Specimens thought most likely by the excavators to have been artificially fractured were found in a red pebble bed some ten metres down, where was also found the fragmented carapace of a giant tortoise, and also from the western end of the north face. In the pipe in the *nari*, known as "the chert plug", containing a quantity of angular chert blocks set in red clay matrix, occur many examples which have been fractured *in situ* by pressure. The scars are quite fresh and in several instances the pieces which had been removed were only a few millimetres away.

The collection also contains four fragments of freshly broken hard limestone, pink in colour and one chert fragment showing a bulb of percussion. These are labelled as coming from the bone area on the north side of the excavation, where was a fan-shaped mass of clay. They appear to be geological samples collected by the excavators and so have not been included in the analysis.

C. *The Categories*

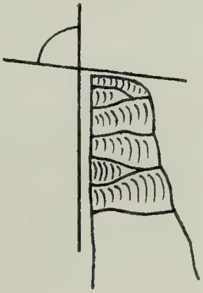
Definitions :

The following terms have been used in the text as defined below.

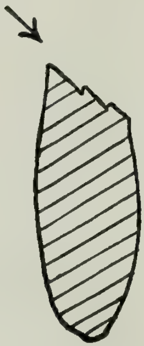
1. Specimens have been approximately classified according to shape when laid flat on a table as follows—

    Sub-rectangular
    Square .
    Triangular
    Oval .
    Irregular (Not falling into any of the above categories.)

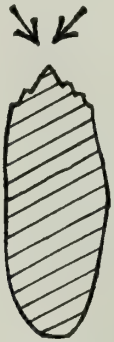
2. Length—the length of the longest rectangle into which a specimen can be fitted.
3. Breadth—the breadth of this rectangle.
4. Flake—exhibiting a striking platform, bulb of percussion and other characteristics of percussion or strong pressure flaking. Length-breadth ratio between 5 : 2 and 5 : 5.
5. Psuedo-flake—apparently exhibiting a main flake surface but with no surviving evidence of striking platform, bulb or concentric rings.
6. Flaking- or platform-angle—the angle made by the striking platform and the main flake surface.
7. Angle of edge-flaking—the average angle made by the intersection of the under or main flake surface with the edge trimming on the upper face, i.e.



8. Unilateral flaking—that which is directed from one face only, i.e.



9. Bilateral flaking—that which is directed from both faces of the specimen on the same part of an edge, i.e.



10. Multi-directional flaking—that which is exhibited by specimens that have been flaked from more than two directions.
11. Eolith—fractured flints from " Pre-Glacial " plateau drift and the East Anglian Crags which were at one time considered to exhibit human workmanship but which today are generally agreed to be natural, having been flaked by soil creep and pressure.

In the following analysis of the material every specimen collected has been noted and included in the tables irrespective of whether it exhibits any fracture or not. The percentage of unfractured specimens to the whole collection is of course very much larger than the table indicates since it was clearly impracticable for the excavators to preserve everything in this category. The measurements of those preserved are, however, useful for comparison with the fractured specimens. For analysis specimens have, therefore, been divided into five groups :

		Percentage of total
(1) Unfractured specimens	85	27·3
(2) Thermally fractured specimens	11	3·5
(3) Specimens on tabular chert	37	11·8
(4) Specimens on nodules and lumps	103	33·2
(5) Flakes and pseudo-flakes	75	24·2
Total	311	

(1) *Unfractured Specimens* (85)

These consist predominantly of much weathered and rounded concretions of chert, limestone or iron-stone and show no evidence of any localized battering or abrasion. A few pebbles are included but these are more in the nature of rounded, sub-angular pieces of chert and limestone rather than river cobbles. A few fragments of tabular chert and limestone also come into this group. It is likely that many more such pieces were found in the deposit, especially in those parts adjacent to the *nari* or scree where angular limestone blocks were most numerous.

Length	Maximum 15 cm.	Minimum 3 cm.	Average 4·5 cm.
Breadth	,, 10 ,,	,, 2 ,,	,, 4·3 ,,
Thickness	,, 8 ,,	,, 2 ,,	,, 3·4 ,,

(2) *Thermally Fractured Specimens* (11). Plate 18, figs. 1 and 2

These are mainly fragments of tabular chert, sub-rectangular or oval in shape and with rounded edges. Most show evidence of a thickish patina, white to cream in colour, which has been reddened presumably due to fire. Some specimens show incipient surface gloss. Five specimens exhibit typical closed ring and cup fracture accompanied by a mottled grey to purple patina. Two specimens show the crackle markings resulting from incorporation in a fire while from another heat spalls have been removed from both faces giving the appearance of bilateral flaking. A few of the specimens in the other categories also show clear evidence of thermal fracture as well as that from other causes. In addition it is strongly suspected, but cannot be proved, that a number of the " pseudo-flakes " listed under group (5) below had their flake surfaces produced by heat fracture.

There is no evidence that any of these specimens were fractured by fire after incorporation in the gravel in the sink. Rather is there every indication that the fracture had occurred before they found their way into the deposit. It is suggested, therefore, that bush fires were the probable agency for the fracture of these specimens. The action of such fires in the splitting and cracking of rocks can be readily observed in the field in the tropics.

(3) *Specimens on tabular chert* (37). Plate 18, figs, 3–7

These are mainly small fragments of no consistent shape and the angle of intersection of the edges with the two faces is very often nearly a right-angle. The edges of most of them show steep " nibbled " working intermittently all round the specimen.

It is noticeable that frequently this retouch has been directed sometimes from the one, sometimes from the other face, but very rarely from both faces at once to produce normal bilateral flaking. Notching is a common feature, again associated with " nibbling " and bruising directed from one face only. It is apparent that the " all-round retouch " on these specimens was not produced at one time, since the degree of weathering or freshness and the patina are variable. Only a few examples show quite fresh fractures or fresh " nibbling ". It would seem, therefore, that most of this " nibbled " working must have taken place before the specimens became incorporated in the sink and that it is only the fresh fracturing that took place after or at the time of this event. Since there is no indication that the fauna, which was interstratified with the chert specimens, can have moved much once it had found its way into the sink, it may be assumed also that the only agency that could effect fracture of rocks *in situ* in this deposit would be pressure, aided perhaps by some collapse of the floor of the sink and by frost action.

By far the largest number of the tabular specimens can be classified as sub-rectangular in shape. Eight are triangular, six are oval, one is square and five are irregular. Measurements are as follows :

Length	Maximum	12·5 cm.	Minimum	3·7 cm.	Average	6·7 cm.
Breadth	,,	9·5 ,,	,,	2·4 ,,	,,	4·6 ,,
Thickness	,,	5·7 ,,	,,	1·0 ,,	,,	2·5 ,,
Angle of edge flaking	Maximum	98°	Minimum	50°	Average	84°

Eighteen specimens show trimming from one or part of one face only while nineteen have the edges trimmed intermittently from both faces—sometimes from one, sometimes from the other, but rarely from both faces at once. Three of these specimens exhibit fresh or near fresh fracture and only incipient bruising or " nibbling " of the edge. The angle of edge flaking in these last is low, between 61° and 79°. It is probable that the absence of continued pressure on the edges of these specimens had preserved them from reduction to the near right angle found in most of the other specimens.

(4) *Specimens on nodules and lumps* (103). Plate 19

These vary considerably in size but on average agree well with the first group. The majority are angular nodules showing signs of bruising and abrasion such as results from eluvial action and it is clear that they must have received this treatment prior to their inclusion in the sink. Again, however, a prominent feature is differential abrasion and patina and this weathering undoubtedly came about at several different times. Often the nodule or lump had broken either down the long or short axis or even along both and the sharp intersections so produced have in their turn been subject to pressure, percussion fracture and bruising. Measurements are as follows :

Length	Maximum	17 cm.	Minimum	2·4 cm.	Average	6·2 cm.
Breadth	,,	13 ,,	,,	2·3 ,,	,,	4·8 ,,
Thickness	,,	9·5 ,,	,,	2·0 ,,	,,	3·7 ,,

Most of these nodular specimens have no particular shape and so have been classed as irregular (50). Some, however, are more uniform; 22 can be described as sub-rectangular, 23 are oval and 8 triangular in form. Edge-trimming is from one side only in 38 specimens and from two or more faces in 53. In the remainder there is no clear trimming from an edge.

Angles of edge flaking (measureable only on 76 specimens) vary from 42° to 107° with an average of 91°.

There is a marked absence of any opposed alternate flaking of an edge such as is found on the Pre-Chelles-Acheul tools of Oldowan and developed Kafuan type. On two specimens only (Plate 19, figs. 5, 6) is there any evidence of this and in both it is apparent that the flakes have been removed at quite different times with a resulting difference in physical condition.

Evidence of percussion fracture can be seen definitely on three specimens only. One abraded specimen has been struck in the centre of one side, the blow removing a flake from part of this face and producing a semi-cone of percussion (Plate 19, fig. 1). On one quite fresh and unabraded specimen a cone of percussion indicates that the block of chert from which it came must have been struck fairly heavily to produce a cone of this size (Plate 19, fig. 2).

The most "evolved" form is a heavily leached and white patinated specimen which approaches the "rostro-carinate" type of eolith, with a flat base (or ventral surface) and a high back (or keel) giving it a triangular cross-section (Plate 19, fig. 6). The flaking on this specimen, however, shows differential physical wear and has been directed in most cases from the ventral surface.

(5) *Flakes and Pseudo-flakes* (75). Plate 20

Only fifteen specimens show a striking platform and bulb of percussion, thus preserving a flaking-angle that can be measured. Only this number, therefore, give clear evidence of having been produced either by percussion or by pressure (Plate 20, fig. 1). In every other case, either later fracture has removed the bulb and platform (Plate 20, fig. 2), if indeed these existed, or the "flake" surface is flat and smooth and shows none of the unmistakeable evidence of percussion fracture. Such specimens are referred to here as pseudo-flakes (Plate 20, fig. 3).

Some of these flakes may be of the kind obtained in the initial flaking of a pebble either by nature or man, although the Bethlehem specimens show no clear evidence of this. In such cases either a much restricted bulb and bulbar scar are present or, if the rock is coarse-grained, shatter lines and crushing at the point of impact betray the nature of the force that produced the fracture. In these cases the angle between the flake surface and the pebble cortex is an acute one (Clark, 1958).

Since some of these pseudo-flakes present an undulating or wavy flake surface and a total absence of concentric rings, it is suggested that they may be due to thermal fracture. Bush fires, or sudden heating and cooling can produce such splitting of rocks under tropical conditions and, when we take into consideration that they occur with specimens that were unquestionably fractured by fire, it seems probable that fire may also have been responsible for producing a large proportion of these pseudo-flake surfaces.

The measurements of specimens are as follows :

Length	Maximum 17·0 cm.	Minimum 3·8 cm.	Average 7·6 cm.
Breadth	,, 15·0 ,,	,, 0·7 ,,	,, 6·5 ,,
Thickness	,, 6·0 ,,	,, 1·6 ,,	,, 3·0 ,,

Specimens may be classed as triangular (25), sub-rectangular (15), oval (18) and irregular (17) in form.

Platform angles of flakes vary between 81° and 122° with an average of 99°. In most instances platforms are negligible and in only two specimens is there a wide enough platform to indicate that the flake may have been removed by a swinging percussion blow.

The angle of edge flaking measurable on 70 specimens varies from as little as 57° to 96° and the average, as might be expected, is as high as 82°.

In 32 specimens the trimming comes from one face or part of one face only and in 37 flaking comes from both faces. Five examples show no secondary trimming, while only one shows incipient bilateral flaking to form a simple wavy cutting edge.

The edge trimming is steep and is similar to that seen on the tabular specimens.

D. *The Nature of the Flaking*

The above description shows that fracture of the chert specimens in this collection has been brought about in several different ways and at different times.

(i) *By percussion.* The characteristics of percussion fracture—cones and semi-cones, fairly pronounced bulb and concentric rings, and sometimes bulbar scar—are rare in the Bethlehem collection. Twenty per cent. of the flakes show a bulb and striking platform but in most cases the platform is narrow, the bulb is flat and the bulbar scar is absent. Such characteristics are much more suggestive of pressure than of percussion fracture.

Only a small percentage also of the flaked nodules and lumps show true negative flake scars and there is hardly one of these that shows a deep negative scar—unmistakable indication that it has been fractured by direct percussion. Where such a scar is present it is clear that the bulb was invariably shallow, again a feature more characteristic of flaking by pressure.

As mentioned above, however, one fresh lump (Plate 19, fig. 2) shows a very good cone of percussion at one end and another specimen (Plate 19, fig. 1) exhibits a semicone. In the case of the first example fracture must have come about after, or immmediately before incorporation in the sink. The second example was subjected to eluvial abrasion and weathering before inclusion in the deposit. Both these specimens had been struck in the centre of the block—in the first example the blow was sufficiently strong to detach fragments from all round the circumference but in the second it was insufficient to shatter the pebble and only one small flake was removed.

One small nodule (Plate 19, fig. 4) has been split in half but there is no sign that this is the result of percussion. However, this half nodule has been truncated at one end by the removal of a single percussion-struck flake. The edges in some places show incipient " nibbling " such as follows from pressure, induced, no doubt, by the weight of the overlying deposit.

Only 0·7% of specimens show any clear evidence of percussion fracture, therefore.

Recent examination of naturally fractured pebbles in the Batoka Gorge of the Zambezi river has shown that simple and even more elaborate fracture, closely simulating that exhibited by the so-called Kafuan Culture of Africa, can be brought about by rocks falling from a height on to pebbles wedged in gravel below (Clark, 1958). It is suggested, therefore, in the case of the quite fresh specimens from Bethlehem believed to have been struck and fractured by percussion when they were already in the sink, that this fracture was brought about either by rocks or stones falling on to them from above or when they themselves fell into the sink.

Stone that has been subjected to temperature stresses from long exposure on the surface is much more readily split along the lines of weakness than is "fresh" stone, as even the earliest tool-makers were not slow to appreciate. If, therefore, the Bethlehem deposits represent the slowly accumulating fill of a sink brought about by the washing in of eluvial material from the surface above and by gravitation then it is easy to see how the small amount of percussion fracture exhibited by the specimens lying in a deposit which sometimes contains blocks half a metre in diameter was probably brought about.

Even the earliest tool-makers appreciated that if it is required to remove a flake from a stone or pebble to produce a sharp edge it is necessary to strike the pebble a glancing blow away from the centre of the block and not towards the centre as is the case with the two specimens mentioned above.

(*ii*) *By heat.* Most of these specimens had been weathered before they found their way into the sink. In three specimens, however, the cup markings and other evidence of thermal fracture is fresher. It seems improbable that this kind of fracture can have been brought about naturally once the specimens were in the sink. It follows, therefore, that either these three examples became incorporated in the deposit shortly after having been subjected to heating and fracture on the surface or one must invoke human agency. There is no evidence that any Lower Pleistocene hominid knew how to make or use fire and its earliest known use is in the Middle Pleistocene by *Sinanthropus* at Choukoutien (Oakley, 1957). It would seem, therefore, that the fires that produced the Bethlehem specimens cannot have been man made.

(*iii*) *By pressure.* The characteristics of pressure flaking may be summarized as being a small to insignificant bulb, only a very insignificant, or no striking platform, and wavy or rippling concentric rings on the main flake surface. The flakes and blades are generally flat and thin and very often, but by no means universally, microlithic in proportions.

Approximately 57% of the Bethlehem specimens show evidence of pressure fracture. This is of two kinds depending on whether the pressure was strong or weak. Sometimes a sizeable flake has been removed from a core by strong pressure but more often the pressure has been weaker and is confined to "nibbling" along part or all of an edge. The results of strong and weak pressure flaking can be seen on both weathered and fresh specimens. Plate 19, figs. 3, 5, and Plate 20, fig. 1 are examples of primary pressure working. Plate 20, fig. 1 suggests at first that it is a large, percussion-struck flake-blade but the insignificant bulb and near right angle to the platform indicate that pressure and not percussion is more likely to have been responsible. It is the only large specimen of its kind in the collection. The split nodule or pebble illustrated in Plate 19, fig. 5 is one of the very few specimens showing bilateral flaking. The differential abrasion of the aretes indicates, however, that this flaking occurred at more than one time. The shallow scars, rippling of the concentric rings and parallel nature of the negative scars on the one face show that pressure was most probably the agency that removed these flakes.

Plate 19, fig. 3 is a quite fresh, flat, triangular piece of chert having a superficial resemblance to a micro-blade core in that one, probably two, bladelets had been removed from the apex down one edge. Some bruising of the opposite end of the specimen indicates, however, that these blades were almost certainly removed by pressure onto the apex from above thus forcing the blades from the edge of the fragment which must have been wedged in a vertical position in the deposit.

"Nibbled" flaking of edges, or parts of edges by pressure can be seen in a high proportion of the specimens in the collection. This is particularly well demonstrated on the tabular chert specimens (Plate 18, figs. 2–7) and on a proportion of the flakes and pseudo-flakes (Plate 20, fig. 2). Both weathered and fresh specimens with "nibbled" pressure flaked edges are found. In most cases the flaking has not all been done at the same time and takes the form of simple notching and concave edges such as may result from the compaction of a bed of angular gravel under pressure.

E. *Comparisons and Conclusions*

It is apparent that direct percussion (0·7%) played a very negligible part in the fracturing of these cherts. On the other hand thermal fracture is conclusively proved for 5% of the specimens and is strongly suspected to have been responsible for a much higher proportion (for example many of the pseudo-flakes) though this cannot be confirmed with certainty. The great majority of specimens have been fractured by pressure, mainly applied to the edges of flakes, pseudo-flakes and tabular fragments so as to produce steep angles of edge-flaking.

The late Mr. Hazeldine Warren made a detailed study of the ways in which this type of fracture is brought about in nature and clearly demonstrated, both by experiment and in the field, how pressure from the weight of overlying deposits or their gradual compaction, collapse and movement due to soil creep or solifluction were the main causes of fracture of the East Anglian and other " eoliths " (Warren, 1914). The Bethlehem specimens present similar features of natural pressure flaking (notching, " nibbling "and multi-directional flaking) and indeed such fracture is demonstrated beyond all doubt in the natural fragmentation of blocks in the " chert plug " at this site.

Typical fracture of this kind is found also in tropical and sub-tropical regions in the vicinity of pans and water courses or on specimens incorporated in scree or spread out over flats adjacent to the source of supply of tabular rocks such as flint, chert, chalcedony, indurated shale or ironstone. Much of this kind of steep " retouch " can be shown to be the result of natural causes as listed above but some of it, sometimes, is certainly humanly produced. This can be seen, for example, in industries of Hope Fountain-type from Africa south of the Sahara or in the Khargan and Epi-

Levalloisian industries of the Kharga Oasis in the western desert (Caton-Thompson, 1952). Even so, it is by no means certain that natural agencies have not played some part in producing the all-round " nibbled " and steep retouch observed on tools belonging to some of these industries; for example on many of the tools from the scree deposits at Hope Fountain itself or at Gwelo Kopje in Southern Rhodesia (Jones, 1929). This can be checked against similar industries from other sites where natural fracture can be excluded and where it can be seen that the angle of edge flaking is much more acute (Clark, 1960).

However, at least a few sites in Africa remain where the angle of edge flaking on these " nibbled " flakes is characteristically steep (i.e. Broken Hill, lowest floor (Clark, 1960) ; Olorgesaile(Posnansky, 1959) and Isimila (Howell, Cole & Kleindienst, 1959)), where man, not nature, was the tool-maker; In Europe the same can be said for a proportion of the secondary trimming of flake tools of the Clacton industry from the type site (Warren, 1951).

In each of these industries there is abundant proof, however, of percussion fracture and the intentional production of flakes from cores.

At Bethlehem, on the other hand, the almost complete absence of characteristic percussion flaking would seem to rule out human agency as the cause of the fracture of the chert specimens. The pseudo-flake surfaces are most probably of thermal origin while the differential patina and wear point to movement in eluvial gravel and scree before and pressure of overburden after incorporation in the sink, as being the two main ways in which they were broken and " retouched ".

Barnes' (1939) isolation of the angle platform-scar as being one of the most significant criteria in distinguishing between naturally and humanly fractured stone is fully confirmed by the Bethlehem analysis. The term *angle of edge-flaking* used earlier by Hazeldine Warren has been adopted here, however, since it conveys more clearly the nature of the angle under consideration and obviates any confusion with the *platform angle*. Statistical comparisons of the angles of edge-flaking of the Bethlehem specimens were made, therefore, with the following collections in order to try to determine where the closest similarities lay—East Anglian "eoliths", Lower Eocene flaked flints, Kafuan specimens from the Kafu river, Uganda, Pre-Chelles-Acheul flaked pebbles from the Kalomo river, Northern Rhodesia and flake-tools of Late Acheulian Age from Kalambo Falls, Northern Rhodesia. Comparison was also made between the lengths and breadths of Bethlehem flakes and pseudo-flakes with those of the Late Acheulian flake-tools from Kalambo Falls. Acheulian flake tools were selected for this comparison because there is no doubt as to their having been made by percussion fracture and retouched, sometimes steeply, by man. Since the total number of specimens from Bethlehem was only 311 and only 180 of these exhibited flaked edges of which the angle could be measured and since the number of eoliths, Eocene and Kafuan specimens, available to the writer for comparison were also small, the results must be considered as indicators of probability only, though it is not anticipated that they would be greatly different were fully representative samples available.

Plate 21 shows histograms of the frequency distribution of angles of edge-flaking of the Bethlehem specimens and the five groups listed above.

The greatest number of angles of edge-flaking at Bethlehem are between 80° and 90° and the same can be shown to be the case for the East Anglian eoliths and the small number of Eocene specimens.

On the other hand, the angles of edge-flaking of the Acheulian tools lie most frequently between 55° and 65°, thus confirming Barnes' findings for eoliths, natural fractures and sixteen human industries (Barnes, 1939). There can be no doubt that the associations of the Bethlehem specimens are with the naturally fractured forms. On the other hand, the Kalomo pebble tools have the greatest frequency between 65° and 75° with a minor peak between 82° and 84° and the Kafuan tools from Uganda show two frequencies—between 60° and 70° and between 80° and 90°. This it may be suggested, though the sample is insufficient to prove it, indicates that the so called Kafuan Culture is in part the result of natural and in part due to deliberate fracture ; it is thus in general agreement with Bishop's (1959) analysis of Kafuan split pebbles though, as the latter points out, such intentionally fractured pebbles as do occur with these Kafuan assemblages are usually *on* not *in* the gravels and so are of Upper Pleistocene age. It would seem from the histogram of the Kalomo tools that these belong with the humanly fractured groups as is to be expected, though the percentage of specimens with angles between 80° and 90° suggests that a number of these also may have been fractured by natural causes.

Comparison of the lengths and breadths of the Bethlehem and Kalambo Falls specimens (Plate 22) shows that these are more concentrated and less dispersed in the humanly worked tools. This greater variation and diffusion of the Bethlehem examples can be seen again when plotted graphically Plate 23. These patterns can probably be interpreted as, on the one hand, confirming the intentional nature of the human flaking which shows itself in the use of a traditional technique thus limiting and concentrating the frequency distribution of the flake form and on the other emphasizing the absence of any such intentional technique and the proof of the existence of more than one agency of fracture for the Bethlehem specimens.

Such comparisons confirm the evidence from the detailed observations and measurements given above, that all the Bethlehem specimens are naturally fractured and that there is no indication from any of them that an early tool-making hominid was living in this region contemporaneously with the Villafranchian fauna. This conclusion is based on the following characteristics which, when found in combination in collections of earlier Pleistocene age, can be taken as forming conclusive proof that a non-human agency has been responsible for their fracture : Absence or very low percentage of flakes with striking platforms and bulbs of percussion, high angles of edge-flaking, "nibbling" and notching of edges by pressure, multi-directional, but very rarely bilateral flaking, differential abrasion and patina of flake scars, the rarity of percussion flaking and general frequency of pressure flaking.

While, therefore, no evidence can be deduced from the Bethlehem chert collection that their fracture was due to any agency other than nature, this does not exclude the possibility that some of those with suitably sharp edges could have been *used* by some early hominid of Australopithecine form. In this connection it is of interest that Dr. Stekelis recovered during his 1940 excavation a number of broken bones of which he says :

> " Special attention was paid to a number of broken bones, belonging to small animals. All these bones are broken in the length and some of them bear marks of ' working '. One piece, having a polished edge, is especially remarkable and may be considered to be an awl. If this piece had been discovered in a Paleolithic cave, it would no doubt have been assumed to have been worked with by man. The whole collection amounts to about 30 pieces. For lack of any material to compare them with, I can say nothing more about these broken bones. The bones cannot be considered to have been broken by animals, as, for example, hyenas, as they bear no toothmarks. They may have been broken by pressure ; still, the facts that the breaking is always in the length and that the second part is always missing, do not allow the conclusion that the breaking was done by pressure ; and it almost appears as though the bones were broken for the purpose of extracting the marrow contained in them."

These bones are presumably still in the Palestine Archaeological Museum and it would be of considerable interest to examine them in the light of Dart's " Osteodontokeratic Culture " associated with *Australopithecus* in South Africa (Dart, 1957) If evidence of their intentional fracture can be confirmed it could be that some of the thermal fractures seen on the Bethlehem cherts might show that here man was a fire *user* also.

APPENDIX

GEOLOGICAL REPORT ON THE ELEPHANT PIT, BETHLEHEM

By S. H. SHAW

DESCRIPTION

The main excavation has been in a gravel deposit consisting of angular flint debris (varying in size from fragments a few millimetres in their maximum dimension to blocks 30 cm. or more across) embedded in stiff red or brown clay. It is in this gravel that the bones have been found. In the south wall of the pit this gravel bed is seen to be steeply banked against a more chalky deposit which varies from a fairly solid chalk to a breccia of chalk fragments. This chalky rock is penetrated by fan-like streaks and pockets of red clay with small angular flints.

The red and the brown clays are both very stiff and have a wax-like texture when freshly taken from the ground. They show no sign of any bedding and on washing yield a residue of tiny angular fragments of flint which range down to microscopic size. The brown clay shows frequent films of black manganese dioxide on broken surfaces but this feature was not seen in the red clay.

The macroscopic flint fragments are all angular but without sharp edges. In some cases their edges show flaking and chipping.

The depth of the pit at the time of my visit was 49 feet. The north and east walls of the pit are mainly in gravel.

CONCLUSIONS AS TO THE ORIGIN OF THE DEPOSIT

I consider that this deposit consists of material filling a pipe or pot hole in the chalk that caps the hill at this point. The deposit is therefore a residual one formed practically *in situ* and as a result of the terrestrial weathering and solution of the chalk rock by the agency of rain water.

There is good general evidence to support this view. Chalks of Senonian age occur in the Mount of Olives and run southwards to Bethlehem occupying the high ground to the east of Bethlehem Road. The upper divisions of the Senonian formation contain prominent flint beds and the ground surface is plentifully strewn with flint boulders and stones of all sizes. These are very noticeable along the road to Government House and on the Jerusalem Golf Course to mention only two localities. These boulders do not occur with chalk but clearly represent the results of a long period of terrestrial weathering during which the relatively soluble chalks have been removed by the action of rain water leaving the broken masses of insoluble flint in a clay soil which represents the insoluble residue from the chalk. The Senonian chalks in this district, therefore, are largely covered at the surface by a residual blanket of clay soil with flints probably very similar to the clay-with-flint formation well known in many of the chalk districts of England.

As regards the elephant pit itself, the general evidence given above is supported by the local details which suggest very strongly that at this point the chalk has been locally more soluble and has given rise to a pipe or pot-hole such as are commonly known to occur in chalk formations.

Examination of the pit shows that none of the chalky rock exposed in the pit can be considered as undisturbed or unweathered material. The clay-filled pockets and joints in this weathered chalk are typical of the *in situ* weathering of soft calcareous rocks.

The gravel deposit has clearly been formed at no great distance from the source from which the flints have been derived, otherwise a much greater amount of sorting would have taken place than has been the case. Although the flints have rounded edges, comparison with the general flint debris common in the district suggests that the rounding is not more pronounced than that occurring on pieces that are derived from the residual surface deposits referred to above. It seems certain, therefore, that the gravel represents a scree-like deposit in the emplacement of which water has played little or no part as a transporting agent. The interstitial clay is entirely unbedded and it seems probable that as the pit became deeper as a result of the solution of the chalk, the overlying flint debris descended into the hollow and there became mixed with the residual clay formed by the solution of the chalk.

It is difficult to say whether or not the pit was open at the time the animal remains got into it. A depression or even a local water hole may have existed on the spot but it is just as likely that there was a sudden collapse of the roof once the solution of the chalk had reached a sufficiently advanced stage. It is possible even that the collapse—if it occurred suddenly—may have been caused by the weight of a large animal such as the elephant whose remains have now been unearthed. As the weathering process is a more or less continuous one, the tendency would be for the flint debris to settle gradually deeper and for more material to be added from above.

Such a process of settlement might well account for the shattered state of many of the remains.

In conclusion I append some extracts from Woodward (1912) referring to the occurrence of pipes or pot-holes in England.

> " Such rocks as Chalk, Carboniferous Limestone, may lose, by dissolution in carbonated water, 90 per cent. or more of calcic carbonate." (p. 62.)
>
> " CLAY-WITH-FLINTS
>
> " This term is applied (though not restricted) to an accumulation of unworn flints and red clay that occurs on the surface of Chalk tracts, and lines pipes or cavities, which sometimes extend to a considerable depth. As pointed out by Mr. W. Whitaker, it is a residual deposit due to the dissolution of the Chalk, leaving the flints and earthy matter, which attain a thickness of from 1 to about 5 feet. The pipes extend vertically or obliquely downwards in a more or less circular form, diminishing in size the deeper they occur, and sometimes their extent is indicated in a Chalk-pit by a circular mass or pocket of Clay-with-flints at some depth from the surface, where an oblique pipe has been cut through in the working of the Chalk." (p. 223.)
>
> " Darwin (1881, p. 137, footnote) remarked that the pipes in the Chalk are still in process of formation. ' During the last forty years I have seen or heard of five cases in which a circular space, several feet in diameter, suddenly fell in, leaving on the field an open hole, with perpendicular sides, some feet in depth. This occurred in one of my own fields whilst it was being rolled, and the hinder quarters of the shaft-horse fell in ; two or three cart-loads of rubbish were required to fill up the hole. The subsidence occurred where there was a broad depression, as if the surface had fallen in at several former periods . . . The rain-water over this whole district sinks perpendicularly into the ground, but the chalk is more porous in certain places than in others. Thus the drainage from the overlying clay is directed to certain points, where a greater amount of calcareous matter is dissolved than elsewhere. Even narrow open channels are sometimes formed in the solid chalk. As the chalk is slowly dissolved over the whole country, but more in some parts than in others, the undissolved residue —that is, the overlying mass of red clay-with-flints—likewise sinks slowly down, and tends to fill up the pipes or cavities. But the upper part of the red clay holds together, aided probably by the roots of plants, for a longer time than the lower parts, and thus forms a roof, which sooner or later falls in, as in the above-mentioned five cases'." (p. 64.)

S. H. SHAW.
Geologist.

July 1940

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PLATE 15

A. Bethlehem, general view from the east. The excavation was situated on the highest hill in the centre background. Photograph by E. W. Gardner, 1935.

B. West side of excavation in 1936 showing general nature of the *nari* and gravel junctions.

C. South side of excavation showing slide and vertical junction of gravel and clay at 8 m., 1935.

D. Showing the chert plug (position indicated by ranging rod) in *nari* in southeast corner of excavation in 1936.

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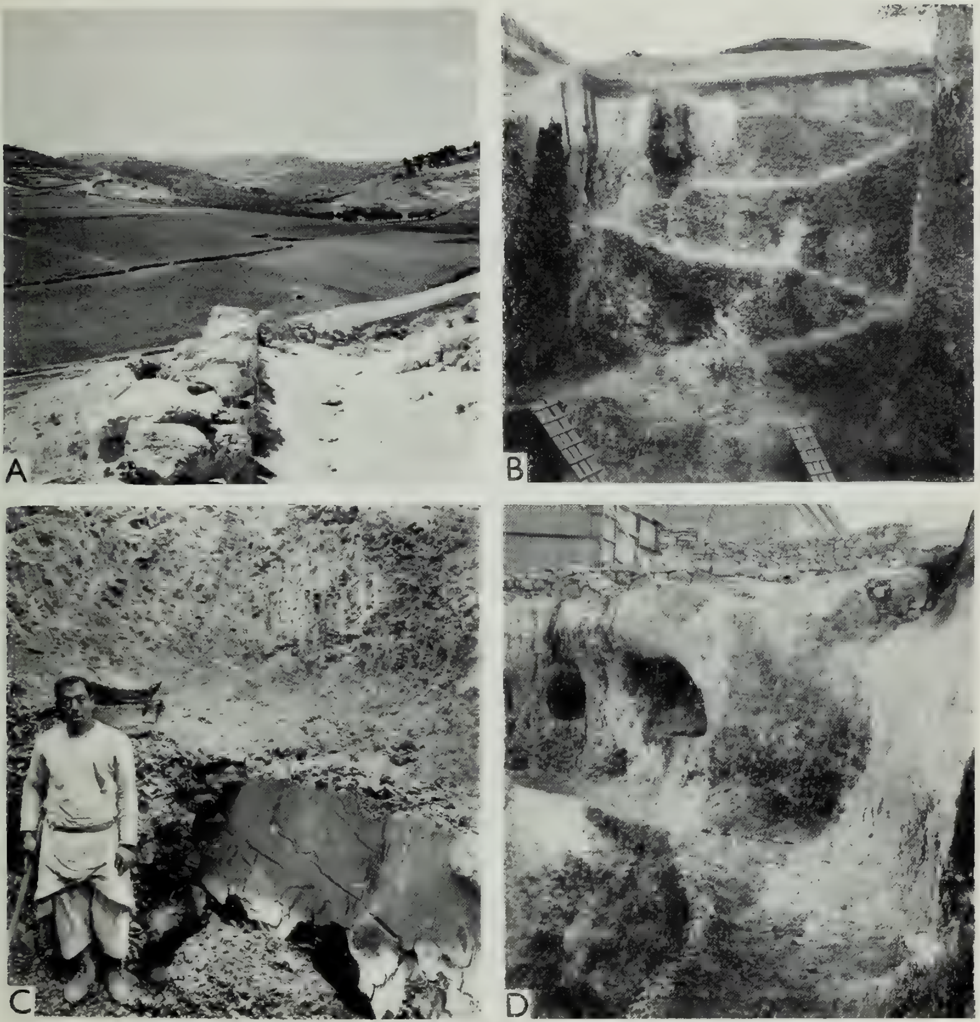
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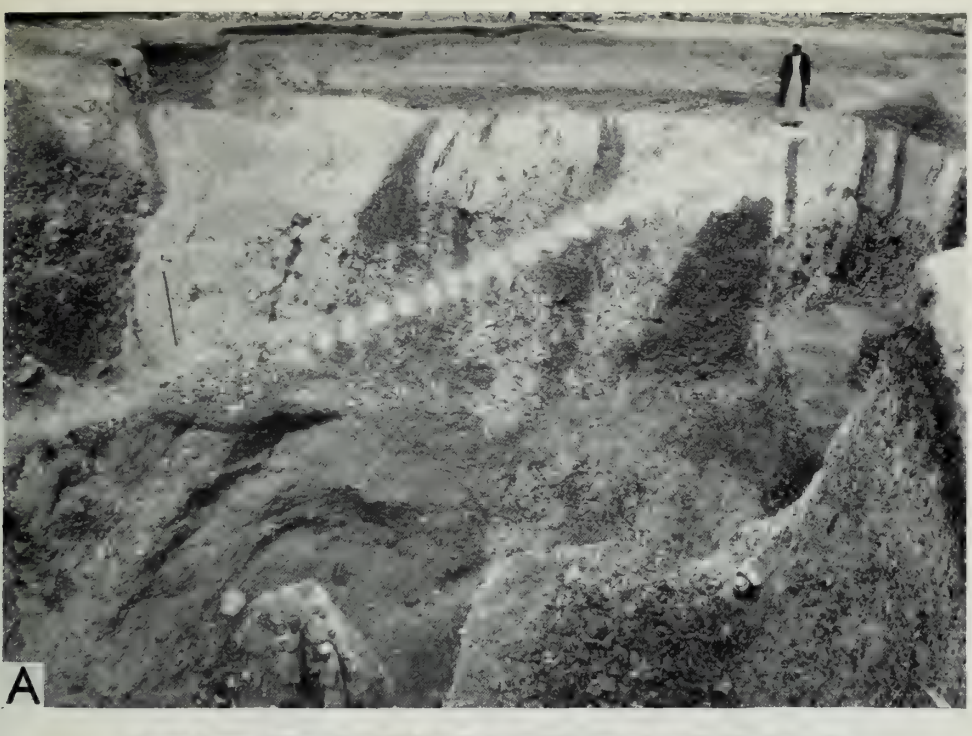
PLATE 16

A. South side and southeast corner of the " Elephant Pit ", excavated to 10 m., showing from left to right chert plug, white chalky *nari*, limestone breccia overlain by *nari* streaked with clay, gravel " wedge ", breccia block and concave slide (in foreground).

B. Detail of junction of gravel and clay on north face of excavation in 1936.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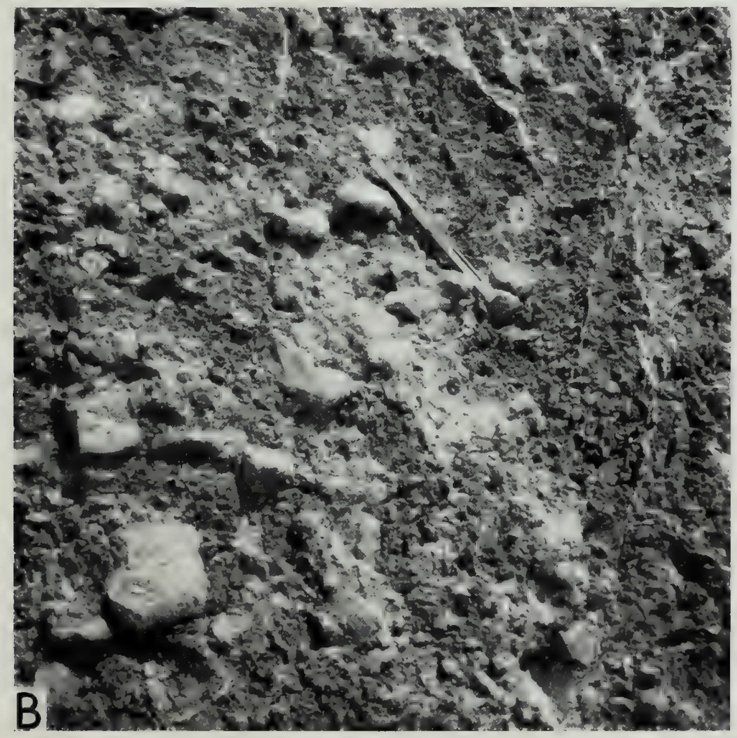
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PLATE 17

Probable north-south section of " Elephant Pit ", Bethlehem.

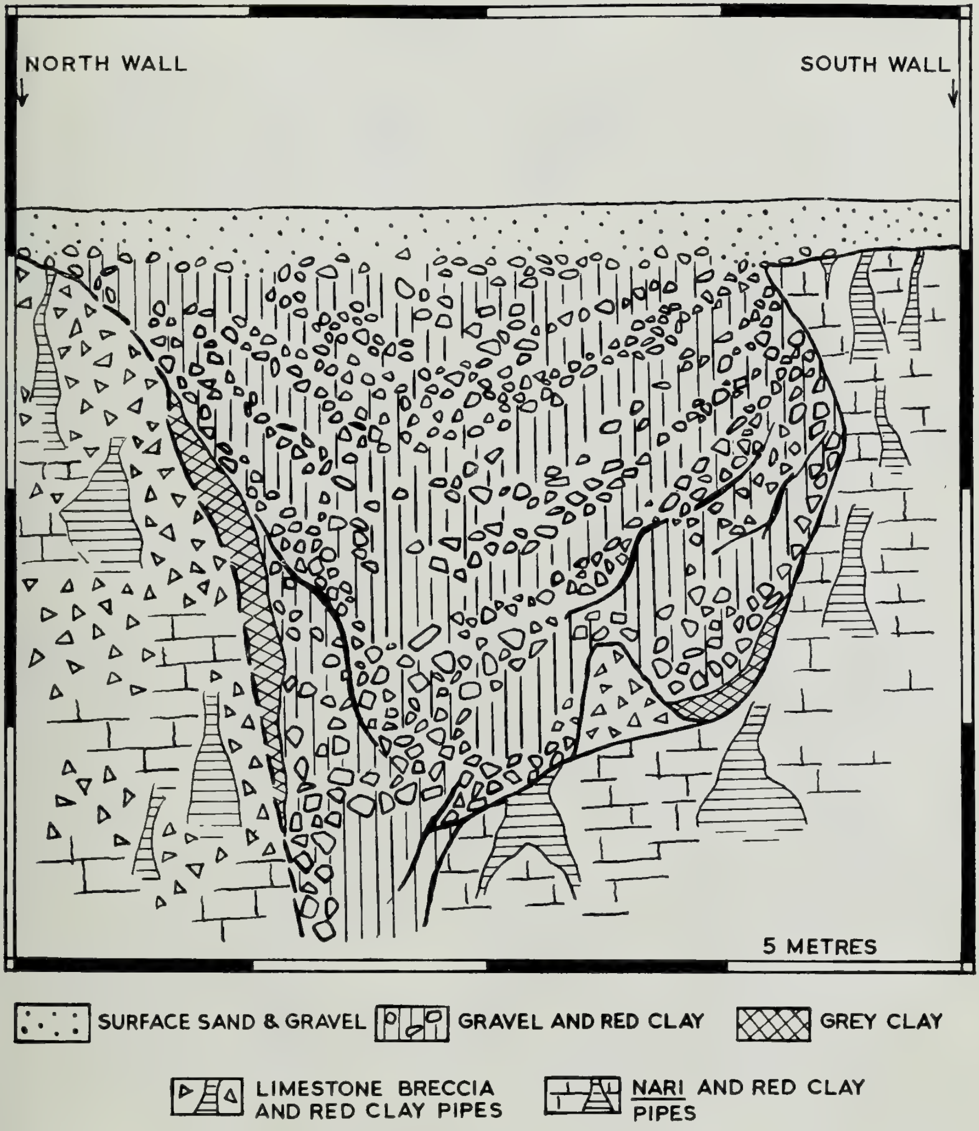

NORTH WALL
SOUTH WALL
5 METRES
SURFACE SAND & GRAVEL
GRAVEL AND RED CLAY
GREY CLAY
LIMESTONE BRECCIA AND RED CLAY PIPES
NARI AND RED CLAY PIPES

PLATE 18

FIG. 1. Fragment of grey tabular chert with thick cream coloured patina reddened on surface by heat: shows cup markings and closed rings typical of thermal fracture, but no flake scars due to percussion or pressure. Condition—fresh and unabraded. E.3772.

FIG. 2. Thermal spall of black to dark brown chert. Remains of thick white cortex at upper end, the surface of which has been reddened by fire. Cup depressions due to heat fracture well seen on both faces. Flaking by pressure has produced two concave nibbled edges. Condition—fresh and unabraded. E.3780.

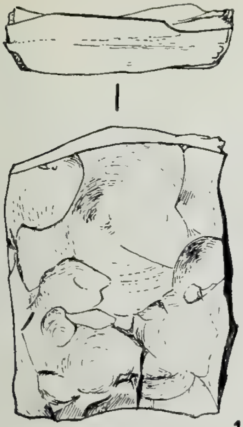
FIG. 3. Small piece of tabular green-grey chert. Roughened cortex with buff coloured patina. Left edge and base show steep nibbling retouch due to pressure. Condition—fresh but edges bruised and abraded by pressure. Bethlehem 32. E.3778.

FIG. 4. Fragment of green-grey chert. The lower face of the piece having split away under heat exhibits thermal closed rings. Thick creamy coloured patina on upper surface, surface reddened by heat. Two scars show where flakes have been removed from the under face probably by pressure. Two approximately opposed concave nibbled edges are present, both resulting from pressure applied from the under face. Condition differentially abraded and patinated, the concave trimming being less abraded than the two faces. E.1709.

FIG. 5. Fragment of grey to green-grey tabular chert. Roughened cortex shows creamy grey patina and signs of iron staining. Pressure applied from both faces to different parts of the edges has resulted in steep " all round retouch ". Angle of edge-flaking is steep, between 86° and 93°. Condition—fresh but edges abraded by pressure. E.3779.

FIG. 6. Fragment of grey tabular chert. One face shows a thick cream coloured patina the other a thinner grey patina; traces of staining by iron oxides. All round retouch by pressure. Steep angle of edge-flaking, i.e. 86°. Specimen has also been subjected to heat, probably before the edges were flaked, which has caused cracking and slight reddening of the surfaces. Condition—edges abraded by pressure. Bethlehem 43. E.3776.

FIG. 7. Probably a piece from a fragment of grey tabular chert. Upper face is composed of flat cortex with differential buff to cream patina. Under face is a fracture surface, probably the result of splitting by heat and shows a green-brown patina. The base and left edge show steep nibbling, notching and bruising retouch by pressure from the cortex face only. The right edge has been bilaterally flaked from both faces to produce a wavy edge formed by two flake scars on the one face opposed against one scar on the other. Patina of this edge is a green-brown, the flaking at the base is unpatinated. Condition—at least three stages of different patina and abrasion. Bethlehem 31. E. 3777.



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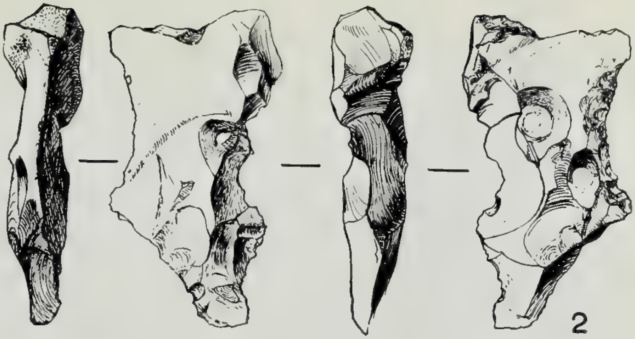

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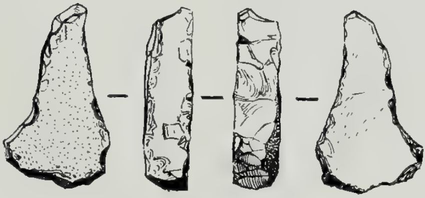

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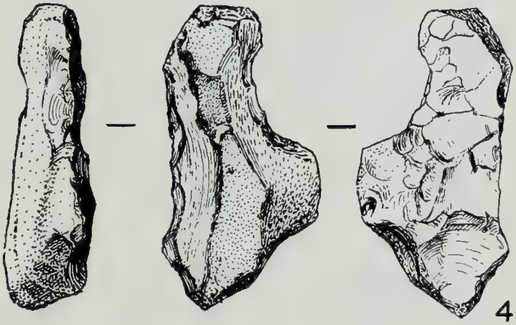

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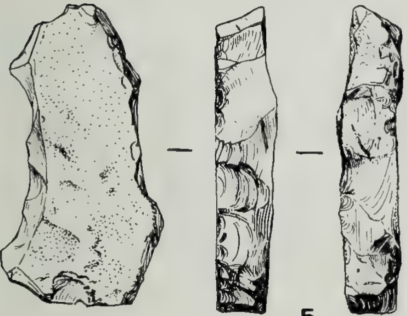

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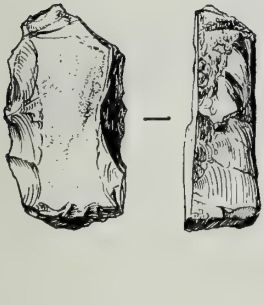

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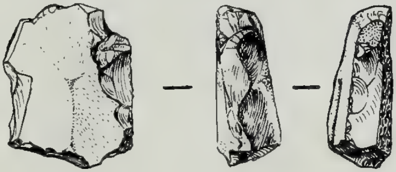

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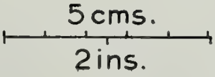


PLATE 19

Fig. 1. Spherical nodule of dark brown chert which has been struck a hard blow by percussion in the centre of one face, thus detaching a flake and producing a semi-cone of percussion. The flake scar exhibits characteristic ripple marks. Dark brown patina. Condition—rolled and abraded. E.3768.

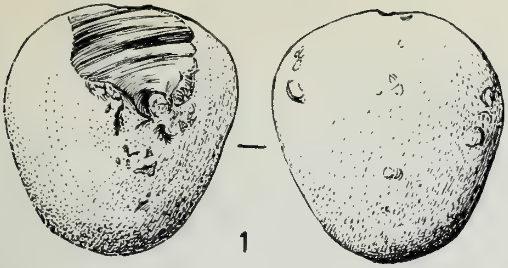
Fig. 2. Irregular lump of chert breccia (mottled white and brown) exhibiting one large cone of percussion and scars from flake fragments that have split away due to the hard percussion blow, directed to the centre of the stone, which fractured the lump and produced the cone. The opposite end to the cone shows flaking from both sides of a ridge, possibly the result of pressure on this end at the same time the fragment was shattered. Condition—fresh and unrolled. E.3548.

Fig. 3. Small splinter of brown chert derived from a weathered nodule ; some cortex at lower end. At the upper end evidence of one, perhaps two, small blades having been pushed off down one edge, probably by pressure applied to both ends of the fragment simultaneously. Condition—fresh. Bethlehem 19. E.3568.

Fig. 4. Split half of an irregular nodule of dark brown chert. The cortex shows some abrasion. The split face shows no bulb of percussion and may be due to thermal causes, but one flake, exhibiting good ripple marks on the negative scar has been removed from the top and at right angles to the split face. Fine nibbling and abrasion of the edges in places due to pressure, otherwise quite fresh fracture. Bethlehem 11. E. 3769.

Fig. 5. Small nodule of green-brown chert which has been split and flakes removed from both faces at one end. Nodule had acquired a cream coloured patina before it was split ; patina of fracture green-brown. Fracture consists of one abraded flake scar on the one face opposed to three or more blade scars on the other and nibbling, battering and bruising of this edge. Good ripple marks can be seen on the blade scars. Condition—differential abrasion and patina of the flake scars show that fracture took place on three or more occasions, the specimen suffering abrasion after each one. The angle of edge-flaking is 54°. This is one of the very few examples of bilateral flaking. Bethlehem 12. E.3770.

Fig. 6. Rostro-carinate shaped specimen in chert breccia (white and grey) that has undergone leaching of the stone and exhibits a white patina. Flaking from the ventral face has removed flakes at intervals round two edges. Some flaking also of the ventral face. The keel or dorsal face shows bruising and battering and some incipient flaking near the nose. Condition—abraded. E.3767.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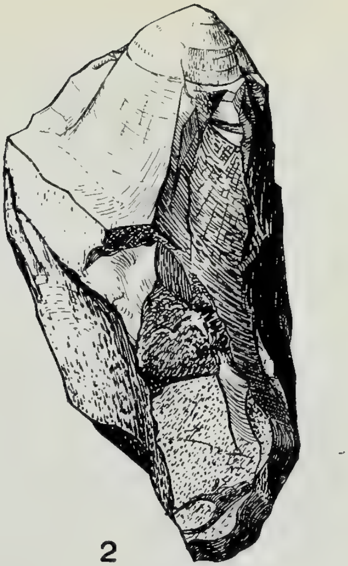
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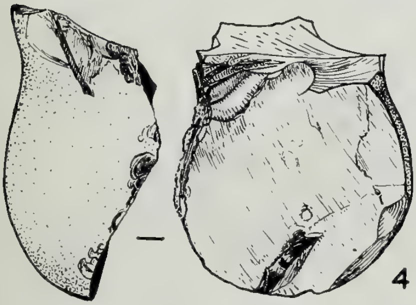
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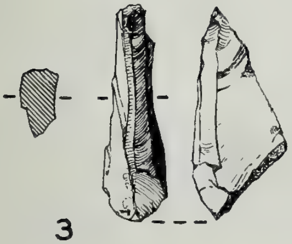
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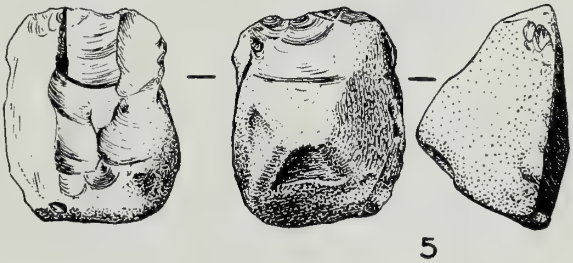
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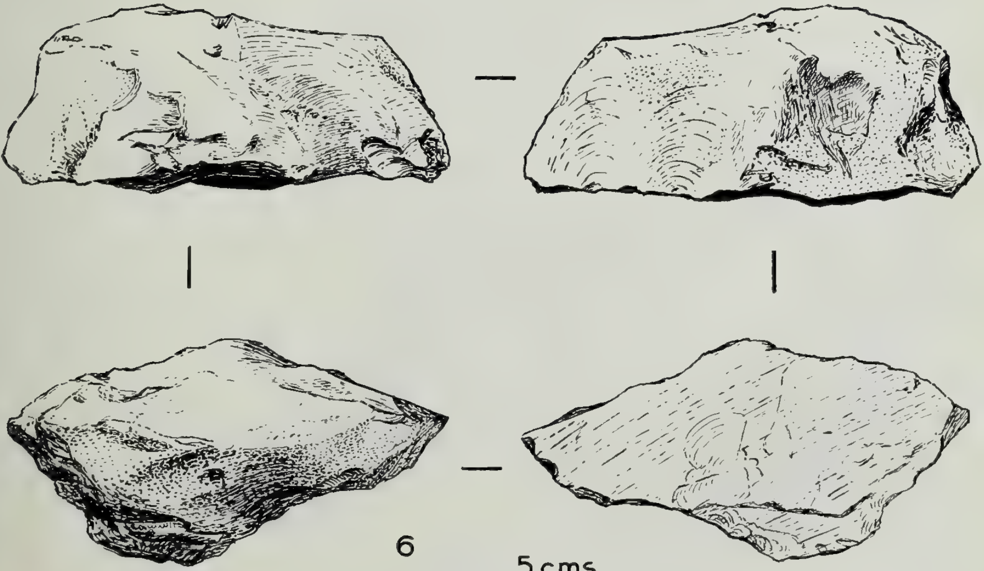
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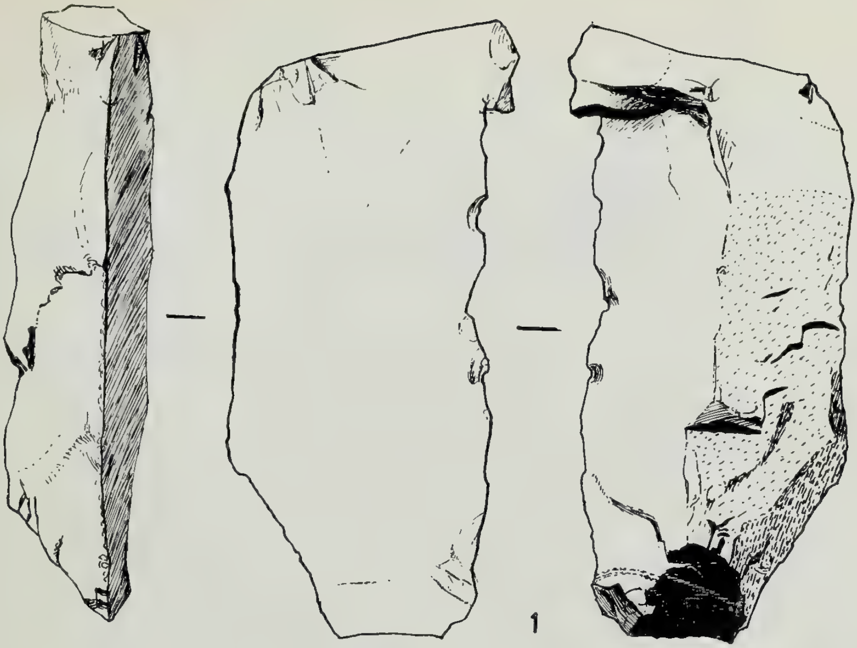
5 cms.
2 ins.

PLATE 20

FIG. 1. Large end-flake of mottled cream and grey chert. Wide striking platform with flaking angle of 91°. Flat and inconspicuous bulb of percussion. The upper face is formed by two fractured surfaces having different degrees of abrasion. These surfaces meet at a central ridge which shows battering. There is no evidence that these surfaces are scars due to percussion or pressure flaking. The upper face is generally more abraded than the under face which is fresh. This shows that the fracturing took place at different times. Bethlehem 49. E. 3540.

FIG. 2. Short thick sub-triangular flake struck from a piece of dark brown tabular chert. Upper face is composed of cream coloured cortex. Under face appears to be a main flake surface though the bulb and striking platform have been removed and parts of two wide flake scars take their place. Nibbled all round retouch by pressure has resulted in a steep angle of edge-trimming, i.e. between 81° and 83°. Condition—the edge-trimming shows a different degree of patina and abrasion from the main flake surface and took place at a different time. E.3543.

FIG. 3. Large psuedo-flake from a rolled nodule or pebble of green chert. The under surface shows no characteristics of percussion fracture and is probably thermally broken ; mottled green-brown patina. Upper face shows a mottled chestnut to white patina. A notch with typical nibbled retouch has been removed from one edge by pressure flaking from the under surface. Angle of edge-flaking is 93°. Condition—under face is more abraded than the notch flaking and the two show different degrees of patination. E.3771.



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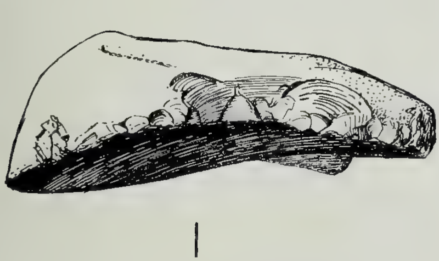

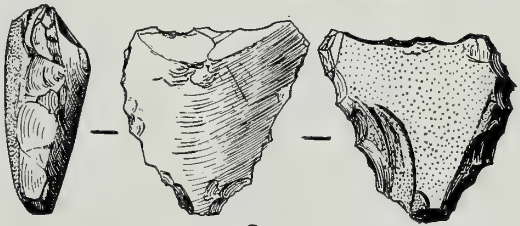

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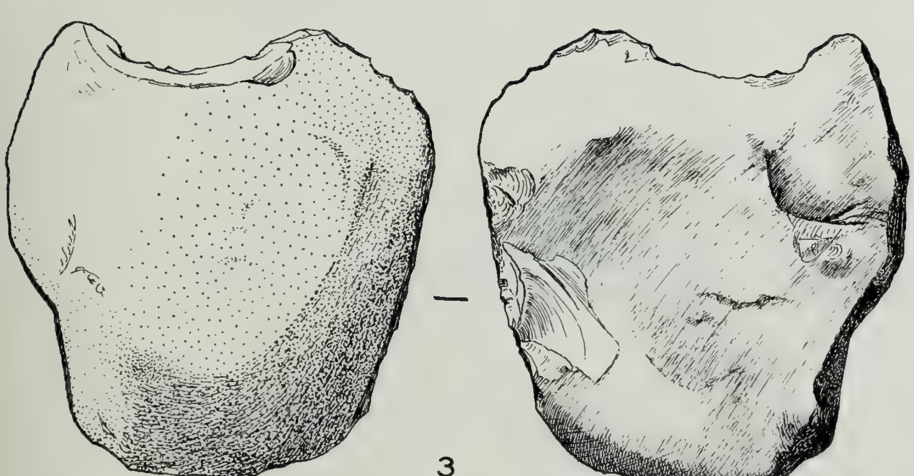

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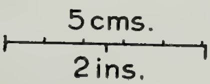


PLATE 21

Frequency distribution of angles of edge-flaking.

FREQUENCY DISTRIBUTION OF ANGLES OF EDGE-FLAKING

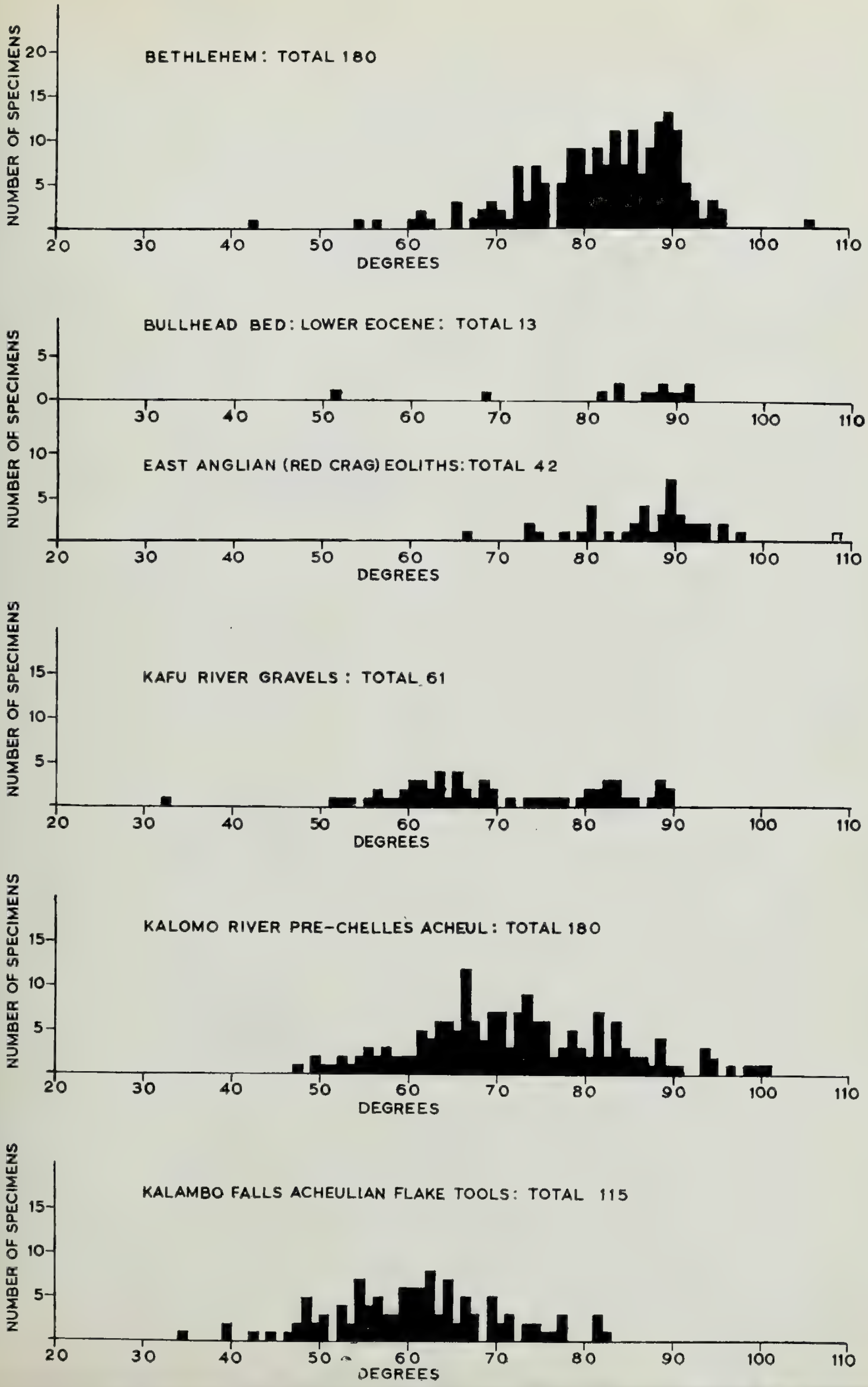


PLATE 22

Frequency distribution : lengths and breadths.

FREQUENCY DISTRIBUTION: LENGTHS AND BREADTHS

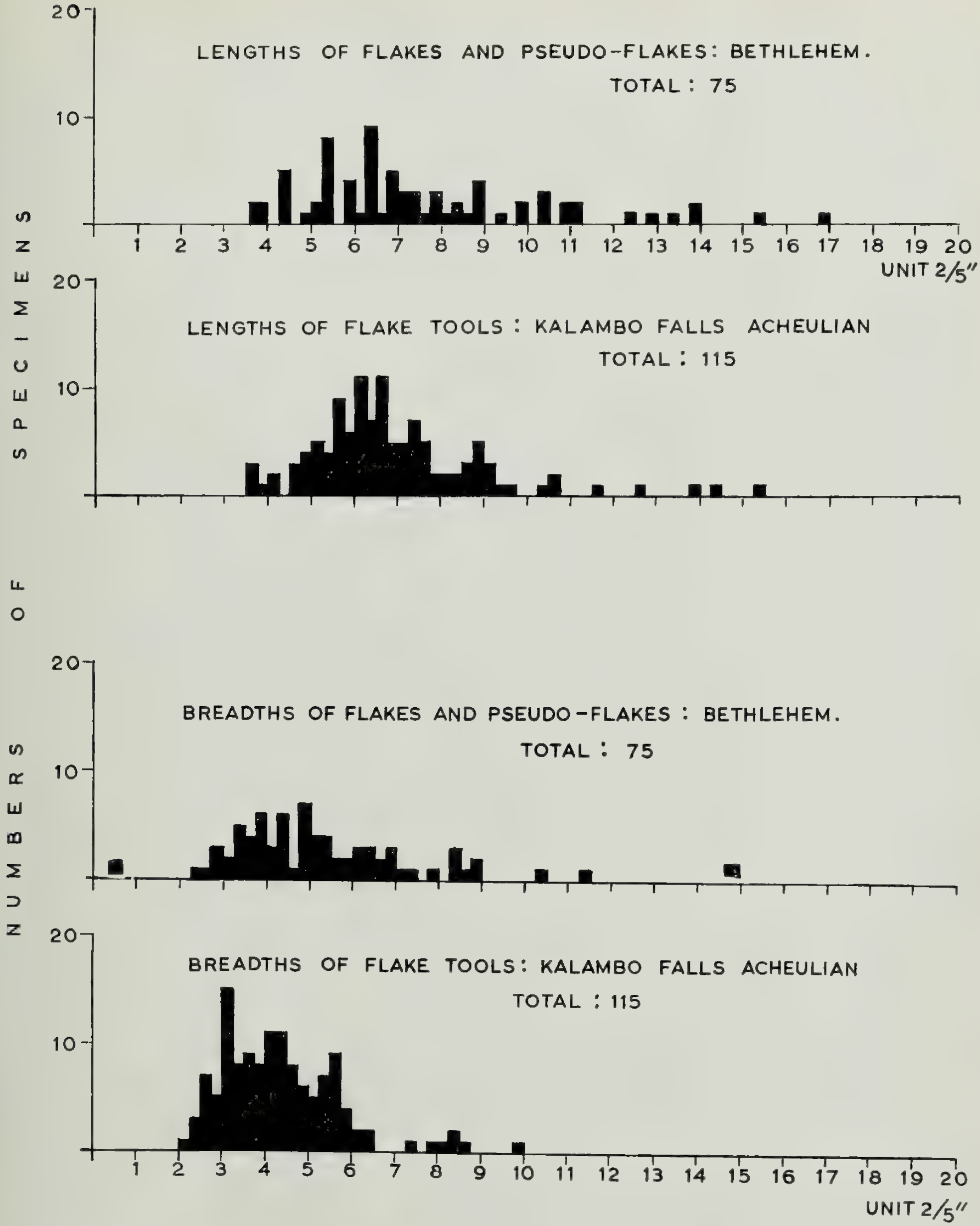
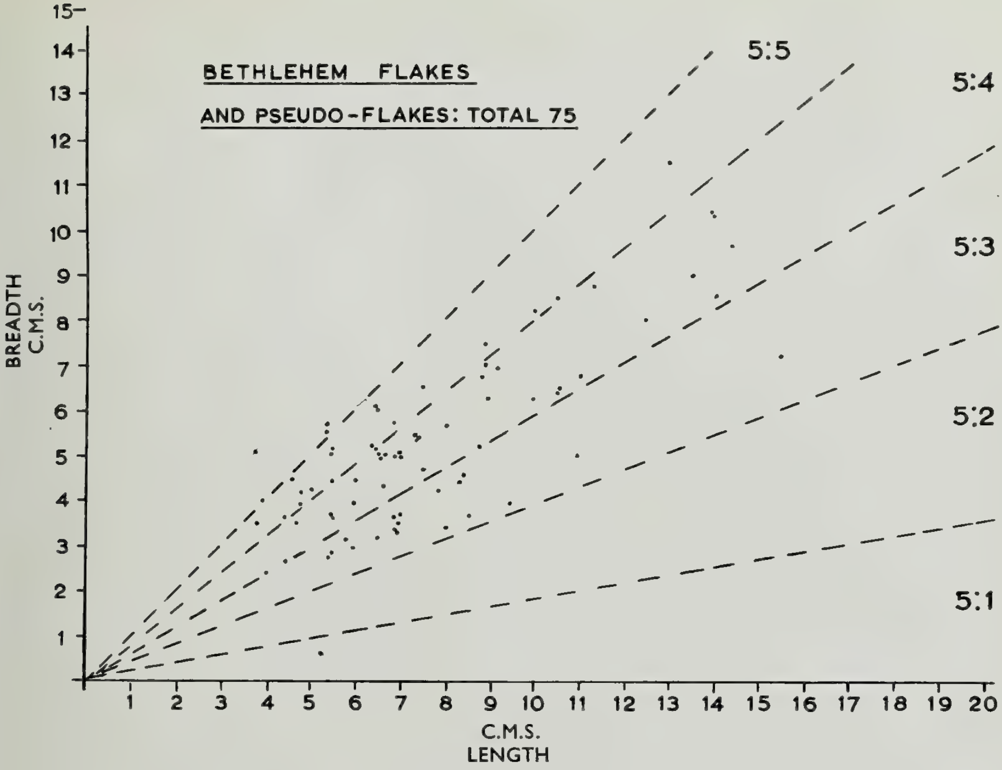
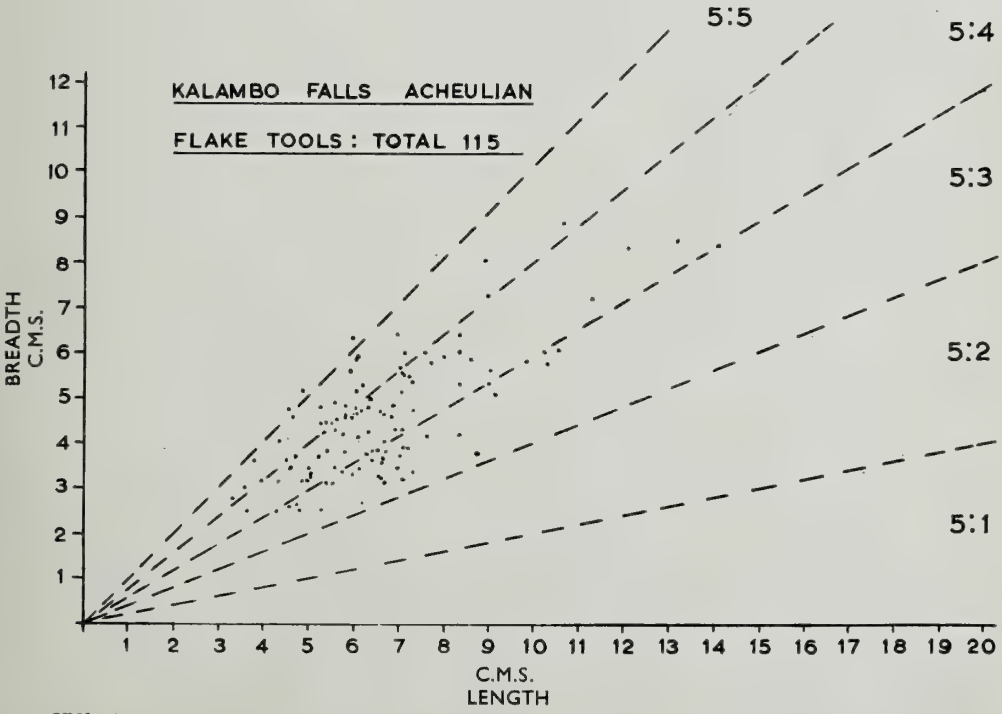


PLATE 23

Length/breadth patterns and ratios

LENGTH / BREADTH PATTERNS AND RATIOS





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M. E. J. CHANDLER

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BY

MARJORIE E. J. CHANDLER

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FLORA OF THE LOWER HEADON BEDS OF HAMPSHIRE AND THE ISLE OF WIGHT

By M. E. J. CHANDLER

SYNOPSIS

The type section of the Lower Headon at Hordle, Hampshire, is briefly described and reference is made to the earlier work on the beds and their flora. The most varied collection of land plants comes from Bed 10 (the Leaf Bed) at Hordle especially east of Beckton Bunny and below Hordle House but gregarious water plants occur at a number of horizons. The mode of preservation of the fruits and seeds is noted. Twenty-seven species new to the flora are added and fifteen genera while some former erroneous generic records have been corrected. Four species formerly described as *Carpolithus* can now be placed in their systematic position. A few sparse records from the Lower Headon of the Isle of Wight are included.

INTRODUCTION

It is over thirty years since the Lower Headon flora of Hordle was studied during which time much new knowledge both of living and fossil material has been gained. The flora has been enriched by more collecting from the type locality at Hordle; there is also sparse material from other sites. Research on older Eocene floras of the South coast has shed fresh light on the relationship of some earlier erroneously determined genera and species so that mistakes have now been corrected. In view of the above considerations the revision of the Lower Headon flora is overdue and is attempted in the following pages.

As always, the author is deeply indebted to Dr. K. I. M. Chesters and Mr. F. M. Wonnacott for their invaluable help in the preparation of this paper.

EXPOSURES OF THE LOWER HEADON BEDS

Beds of Lower Headon age are exposed both on the mainland and in the Isle of Wight: on the mainland at Hordle cliff, near Milford-on-Sea, Hampshire and on the island on its north-western shores. The cliffs at Hordle, unlike most mainland sections at the present day, are still unobstructed by man-made obstacles to collecting although it is clear from the local anxiety about the present rapidity of coast erosion that this state of affairs cannot persist much longer. In the past the condition of the cliff has varied from year to year with major changes extending over long periods. Hence sometimes collecting has been carried out readily, while at other times the productive beds have been inaccessible if high up, or completely masked by scree when low down. In the Isle of Wight a few plants only have yet been found for no rich horizons or pockets with remains of land plants like those of Hordle Bed 10 have so far been discovered.

1. HORDLE

Towards the end of the marine episode represented by the Barton Beds of Barton cliffs recession of the sea was again taking place. As a result the truly marine Barton clays pass gradually through transition beds (the Long Mead End Beds) into the estuarine and fluviatile deposits of the Lower Headon. The land surface must now have extended much further east than during the deposition of the Barton Beds but appears still to have been drained by a now much lengthened river flowing from the west. The variable clays, current bedded sands and lignitic seams of the Lower Headon were laid down by the river which at certain horizons left remains of the plants growing upon its banks in the sediments. These plants are represented by fruits, seeds and battered leaves. At some stages the only plants preserved were the monotonous remains of gregarious genera and species of the aquatic or subaquatic vegetation, e.g. *Chara*, *Limnocarpus*, *Stratiotes* and *Brasenia*, which may be presumed to have grown in brackish lagoons and delta channels in view of their association with estuarine shells.

The most detailed accounts of the Hordle cliff section were those by the Marchioness of Hastings (1852 : 191) and Tawney & Keeping (1883 : 566). During the years 1920–25 the author carried out continuous observation of the section and, as a result, the strata were tabulated so as to show the connexion between these earlier records and the beds then exposed (Chandler, 1925 : 3). With the exception of *Chara*, *Sequoia*, *Limnocarpus*, *Stratiotes*, *Brasenia*, *Rhamnospermum* and rare *Caricoidea* and *Spirematospermum* the plant remains have all been derived from two or three stations at a single horizon named by Tawney & Keeping the Leaf Bed or Bed 10. Because of the action of the sea and the fall of talus, the chance of collecting from a good exposure has been known to change even during a single tide. Thus E. M. Reid related in 1920 how on one occasion she and Clement Reid found abundant remains of *Acrostichum lanzaeanum* exposed in the cliff base and foreshore below Hordle House (now Hordle House School). By the next day the exposure had been completely hidden by a cliff fall. Bed 10 is very variable in character. It consists of sands, clays, lignites and cement stone of limited extent, all of which may yield plants sometimes sparsely disseminated, sometimes concentrated in lenticles or pockets. Its first appearance in the west is at the top of the cliff near Beckton Bunny. Passing eastwards it dips gradually until it reaches beach level a short distance to the east of Hordle House, where it forms the base of the cliff and adjacent foreshore and is about 8 feet thick. Between 1926 and 1931 a magnificent section was exposed in this position by the scouring of the talus from the cliff foot and the shingle from the beach. The constant cutting of the sea into the bed produced a succession of fresh surfaces. Grey tenacious well-bedded clay formed the cliff base and upper foreshore with some interbedded sands. A hard mudstone or cement stone about two inches thick extended laterally for some distance in the foreshore about two feet above the underlying Mammal Bed (green clays with pockets of *Paludina* also well exposed at this time in the lower part of the foreshore). Soft strata immediately overlying the mudstone yielded fragmentary leaf-remains disposed irregularly without reference to bedding planes, the leaves being mangled, twisted and decayed. The carbonaceous films of leaf tissue disintegrated immediately on exposure to dry air, no cuticle having been preserved as in the leaves from Bournemouth or the Hordle *Sequoia* twigs. Hence only impressions are found in old collections and those are liable to be very imperfect on account of the soft matrix. By splitting blocks a number of specimens of *Salvinia* were found. These became hard on drying as often happens when soft strata have been exposed to the action of salt water. In the hardened state the reddish matrix resembles that of the palm leaf (*Nipa*) impressions in the Sedgwick Museum, Cambridge. It therefore seems probable that the palms came from this part of the section. The plants collected from Bed 10 below Hordle House were chiefly representative of a limited freshwater or subaquatic plant-formation. The most abundant genera were *Salvinia*, *Brasenia*, *Stratiotes* and *Limnocarpus*. The few fruits of *Spirematospermum* now referred to a new species, *S. headonense*, were from this site. The occasional patches of *Acrostichum* and (probably from here) of *Nipa* indicate brackish conditions and tropical coastal marshes. The matted occurrence of the *Acrostichum* pinnules here as in the Dorset Pipe-clay Series suggests that it grew where it was preserved, the fronds falling continually into the mud by which they were buried. Land plants were sparse below Hordle House but a few were found by Clement Reid. A small stoned *Rubus* and *Sambucus* were abundant. There were also Icacinaceae and *Zanthoxylum* and a seed of Cucurbitaceae. It is a handicap to further research that at present tons of talus from the overlying Headon and Pleistocene beds obscure this part of the cliff while the foreshore is deeply buried under beach gravel. It may be many years, if ever, before collecting is again possible below Hordle House.

Concentrations of plants have also been seen from time to time in Bed 10 at other parts of the cliff section. A band rich in seeds and twigs of *Sequoia couttsiae* was long exposed east of Taddiford (= Long Mead End) and was accessible a few feet above the beach. It was made conspicuous both by the purplish tinge of its clays and sands and by a bright yellow efflorescence on the surface due to pyrites. There were also plant pockets high up in the cliff between Beckton Bunny and Taddiford but it was necessary to exercise the greatest caution in approaching them owing to the softness of the sands and clays which produce treacherous deep mud flows. Certainly since 1920 and until recent years a most productive lenticle was available near the cliff top a few yards east of Beckton Bunny. Here the richest matrix was coarse purplish sands underlying a few feet of well laminated tenacious purplish-grey clay beneath the Pleistocene gravels. This bed, from six to twelve inches thick, rapidly thinned and finally died out eastwards. In a westerly direction it was cut out altogether by the sloping sides of the stream at Beckton Bunny. The bed yielded remains of trees, shrubs and woody climbers all of which may be presumed to have grown upon the river banks. Endocarps of Mastixioideae, represented especially by two genera, were particularly abundant and could be picked out of the weathered surface in handfuls. The loose sandy matrix was readily sifted on the spot without boiling thus reducing the bulk to be carried home for examination. Water plants occurred more sparsely than land plants.

Towards Taddiford Bed 10 has always been obliterated by a contemporary stream channel cut transverse to the cliff face. The channel is rendered conspicuous by the immense amount of black carbonaceous detritus and masses of broken woody fragments. It did not yield a sufficient quantity of fruits and seeds to be worth working extensively but two good endocarps of *Natsiatum eocenicum* were picked up on rain-washed slopes of talus and there were also *Sequoia* seeds and much abraded fruiting heads of *Protoaltingia hantonensis* formerly referred to *Liquidambar* sp. (Chandler, 1925 : 25, pl. 4, fig. 1).

The Lower Headon fruits and seeds are carbonaceous entities. When first extracted from the cliff they appear as unshrunken and undistorted beautifully preserved specimens scarcely distinguishable except by colour and differences of specific character from their living counterparts. Thanks to the soft carbonaceous and uncrushed condition they are easily dissected so that they afford invaluable evidence about their internal characters. Natural fractures and dissections of such material give readily available information for comparison with broken surfaces in living material. There is always considerable shrinkage of carbonaceous material on drying e.g. large endocarps of *Mastixicarpum* (Mastixioideae) may lose from half to three-quarters of their length in this way. Dried specimens also tend to become distorted and the coarse sandy matrix causes pitting of both external and internal surfaces in some specimens while sand grains may have penetrated along cracks, natural canals and planes of weakness like the edges of valves, filling locule- and seed-cavities and often pock-marking the lining membranes. Testas inside woody endocarps, or tegmens in the case of seeds, are commonly present as tough readily detachable skins. As so frequently happens in carbonaceous material pyrites disseminated throughout the tissues renders them liable to disruption and decay. The softness of the carbonaceous substance may also give rise to crumbling although in both cases deterioration may be delayed by treatment with paraffin wax. Hence the importance of adequate photographic records of the specimens showing range of variation and characteristic features.

The first account of the Hordle flora (Chandler, 1925, 1926) was based on collections by C. & E. M. Reid and by M. E. J. Chandler. A few specimens in the Sedgwick Museum, Cambridge and in the British Museum (Natural History) were also examined. Since that time, in 1939 and 1940, the slope of the cliff near Beckton Bunny made Bed 10 particularly easy to work. Every visit produced valuable material, much being new, and some twenty-seven additions to the published flora were then made. In June 1940 national defence restrictions made further field work impossible and when the coast was once again open in 1945 the cliff was in an unfavourable condition for collecting.

The following are additions to the flora : *Stratiotes hantonensis* Chandler, *Caricoidea obscura* Chandler, *Scleria hordwellensis* n. sp., *Myrica boveyana* (Heer), *Carpinus boveyanus* (Heer), *Moroidea hordwellensis* n. sp., *Becktonia hantonensis* n. sp., *Hantsia glabra* n. sp., Lauraceae Genus ?, *Eoliquidambar hordwellensis* n. sp., Leguminosae (two unidentified genera), *Palaeobursera lakensis* Chandler, *Iodes ? hordwellensis* n. sp., *Icacinicarya transversalis* n. sp , *Icacinicarya becktonensis* n. sp., *Frangula hordwellensis* n. sp., *Meliosma* sp., *Actinidia* sp., *Cleyera ? stigmosa* (Ludwig), *Anneslea ? costata* n. sp., *Eurya becktonensis* n. sp., Thymeliaceae Genus ? *Microdiptera parva* Chandler, *Cornus quadrilocularis* Chandler, *Olea headonensis* n. sp., ? *Acanthus* sp.

Not only have new species been found since the original monograph was published but fresh knowledge both of Recent and fossil material has enabled certain mistakes to be corrected. Just as initially the Hordle flora helped in the understanding of other Tertiary floras examined later, so, too, these other older floras have in their turn shed new light on that of Hordle. Thus it is now possible to place in their proper botanical positions over a dozen species which were before incorrectly named. The following corrections may be noted: *Salvinia hantoniensis* (Chandler, 1925: 10, pl. 1, fig. 1*a–d*; text-fig. 1) has been referred by Shaparenko (1956) to *S. mildeana* Goeppert. *Cladium minimum* (Chandler, 1925: 14, pl. 1, fig. 5*a*, *b*) is now referred to the form-genus *Caricoidea* denoting relationship with Caricoideae rather than with *Cladium* itself. *Limnocarpus headonensis* (Chandler, 1925: 13, pl. 1, fig. 4*a–c*; text-fig. 3) becomes *L. forbesi* (Heer) for reasons given by Chandler 1961*a*. *Campylospermum hordwellense* (Chandler, 1925: 16, pl. 1, fig. 6*a–c*; text-fig. 4) formerly referred to Araceae, belongs to the Theaceae, section Taonabeae, although no identical living genus has yet been found. *Nuphar ovatum* (Chandler, 1925: 22, pl. 3, fig. 3*a*, *b*) thanks to the work of Docturowsky, Nikitin and Korzhinsky becomes *Aldrovandra ovata* (Droseraceae) (see Reid & Chandler, 1926: 111–114, pl. 6, figs. 24–29). *Menispermum obliquatum* (Chandler, 1925: 24, pl. 3, fig. 9*a*, *b*) is transferred to the fossil genus *Palaeosinomenium* (Chandler, 1961: 159). *Rhamnospermum bilobatum* (Chandler, 1925: 30; 1926, pl. 5, fig. 1*a–c*; text-fig. 13) cannot be retained in Rhamnaceae although its relationship is obscure. It has been found now at horizons ranging from the Lower Bagshot to the Hamstead Beds and there is a new and unpublished record from the London Clay. Rhamnaceae Genus ? sp. 2 (Chandler, 1925: 31; 1926, pl. 5, fig. 2) is now referred to *Frangula hordwellensis*. *Corydalis pulchra* (Chandler, 1925: 25, pl. 3, fig. 10*a*, *b*) must be removed from *Corydalis* and the family Papaveraceae and placed in Caryophyllaceae under a new generic name *Hantsia* for reasons given on p. 114. *Liquidambar* sp. (Chandler, 1925: 25, pl. 4, fig. 1) is actually *Protoaltingia hantonensis* common in the older Tertiary Beds of the Dorset and Hampshire coast section as shown by the abraded remains of the fruits with antero-posterior locules and both loculicidal and septicidal dehiscence. *Zanthoxylum ornatum* (Chandler, 1925: 27, pl. 4, fig. 4*a*, *b*; text-fig. 10) is removed from the living genus and placed in a form-genus *Rutaspermum* Chandler. *Actinidia crassisperma* (Chandler, 1926: 34, pl. 6, fig. 2; text-fig. 15) is referred to a new genus *Hordwellia* of the family Theaceae, section Taonabeae. *Carpolithus* sp. 2 (Chandler, 1926: 44, pl. 7, fig. 12*a–d*; text-fig. 28) belongs to the Mastixioideae and probably to *Mastixia*. It resembles *Retinomastixia* Kirchheimer in the numerous resin-cavities in the wall and is named *Mastixia? glandulosa*. *Eomastixia bilocularis* (Chandler 1926: 37, pl. 6, fig. 6*a–e*; text-fig. 20) has to be placed in Zenker's species *E. rugosa*. Ericaceae Genus ? (Chandler, 1926: 37, pl. 6, fig. 7*a*, *b*) is Epacridaceae and is described under a form-genus *Epacridicarpum*. *Symplocoides glandulosa* (Chandler, 1926: 41, pl. 7, fig. 5*a*, *b*; text-fig. 26) and *Carpolithus* sp. 3 (Chandler, 1926: 45, pl. 8, fig. 1*a–e*) both belong to Cornaceae and are now referred to *Dunstania*, a genus from the London Clay which, according to Kirchheimer should itself be placed in *Cornus*. *Carpolithus* sp. 4 (Chandler, 1926: 45, pl. 8, fig. 2*a*, *b*) is referred to *Cornus quadrilocularis* Chandler. Oleaceae Genus ?

(Chandler, 1926 : 42, pl. 7, fig. 7 ; text-fig. 27) appears to be *Olea* and is named *O. headonensis*. *Omphalodes platycarpa* (Chandler, 1926 : 42, pl. 7, fig. 8*a*, *b*) needs confirmation from additional material but no alternative suggestion as to its relationship can at present be made. *Orites* sp. (Chandler, 1926 : 47, pl. 8, fig. 6) : better evidence as to structure and some in regard to the seeds is needed. The fruit spike shows some of the characters of *Carpolithus gardneri* Chandler (see p. 154) ; its relationship still awaits discovery. *Atriplex* sp. (Chandler, 1925 : 21, pl. 3, fig. 2) must be deleted. Further study reveals that it is an accidental Recent inclusion. *Carpolithus* sp. 5 (Chandler, 1926 : 46, pl. 8, fig. 3*a–d*) is referred to Mastixioideae Genus ?

The invaluable detailed studies by Kirchheimer of well-preserved Brown Coal material confirms the reference of *Spirematospermum* to the Zingiberaceae but a consideration of his published evidence necessitates placing the Lower Headon fruits and seeds in a distinct species now named *S. headonense* (p. 108).

The full up-to-date list of Lower Headon plants omitting the Charophyta (described by Reid & Groves in 1921) is given below. All come from Bed 10, just east of Beckton Bunny unless otherwise stated in the systematic description. The numbers by which the beds are designated are those used by Tawney & Keeping (1883) and repeated by Chandler (1925 : 3). Bed 10 has been referred to by C. Reid and by Chandler as the Leaf Bed, Bed 29 as the *Chara* Bed and Bed 31 as the *Limnocarpus* Band of the *Unio* Bed.

In several cases where no new material is available and there is nothing fresh to add to previously published work the registration number in the British Museum (Natural History) is added opposite the name. Where material is no longer extant this is indicated by the word Decayed.

Erdtmann (1960) gave a brief account with figures of three new pollen genera from the *Chara* Bed of Hordle cliff (erroneously said to be in Berkshire). As however a larger work on pollen from the Headon Beds is in preparation by Miss J. Pallot it is left to her to discuss the significance of these determinations. The importance of the discovery of a number of the Hordle plants at other older horizons will be discussed later when work on Eocene floras is surveyed. It is sufficient now to reaffirm that the flora is of tropical [Poltavian] type as indicated by the presence of *Acrostichum*, *Nipa*, Burseraceae, Icacinaceae and Mastixioideae. Associated animal remains also indicate a warm climate, among them are *Trionyx*, *Emys* and *Crocodilus hastingsiae*. There is a rich but little known fish and mammalian element. Among the former *Lepidosteus* scales and *Myliobates* are frequent (see Marchioness of Hastings, 1852 ; Tawney & Keeping, 1883). There are forty-three plant families, at least sixty-seven different genera and eighty-seven named or at least distinctive species.

2. COLWELL

Little collecting has been carried out in the Lower Headon of the Isle of Wight. A few plants only were obtained in the coast section between Colwell and Totland from the *Limnocarpus* Band, a readily recognizable horizon in spite of the fact that it is only a few inches thick. This distinctive band was formerly well exposed at

List of Lower Headon Plants

C, also at Colwell Bay, Isle of Wight. D, also at Downton, Hordle.

Family	Genus and species
Filicales	
Polypodiaceae	*Acrostichum lanzaeanum* (Visiani).
Salviniaceae	*Salvinia mildeana* Goeppert.
Gymnospermae	
Taxodineae	*Sequoia couttsiae* Heer.
Abietineae	*Pinus* sp. (Decayed.)
Angiospermae	
Monocotyledones	
Potamogetonaceae	*Potamogeton pygmaeus* Chandler (C).
	Limnocarpus forbesi (Heer) (C, D).
Hydrocharitaceae	*Stratiotes headonensis* Chandler (C).
	Stratiotes hantonensis Chandler.
Cyperaceae	*Caricoidea minima* (Chandler).
	Caricoidea obscura Chandler.
	Scleria hordwellensis n. sp.
	Genus ?
Nipaceae	? *Nipa* sp. (leaves probably of *N. burtini*).
Araceae	Genus ? (V.20036).
Zingiberaceae	*Spirematospermum headonense* n. sp.
Dicotyledones	
Myricaceae	*Myrica boveyana* (Heer).
Betulaceae	*Carpinus boveyanus* (Heer).
Moraceae	*Chlorophora bicarinata* Chandler. (Decayed.)
	Broussonetia rugosa Chandler.
	Moroidea hordwellensis n. sp.
	Becktonia hantonensis n. gen. & sp.
Caryophyllaceae	*Hantsia pulchra* (Chandler).
	Hantsia glabra n. sp.
Nymphaeaceae	*Brasenia ovula* (Brongniart) (C).
	Brasenia spinosa Chandler (includes *B. antiqua* Chandler).
	Brasenia oblonga Chandler.
Menispermaceae	*Palaeosinomenium obliquatum* (Chandler).
Lauraceae	Genus ?
Droseraceae	*Aldrovanda ovata* (Chandler) (C).
Hamamelidaceae	*Eoliquidambar hordwellensis* n. gen. & sp.
	Protoaltingia hantonensis Chandler.
Rosaceae	*Rubus acutiformis* Chandler.
Leguminosae ?	Genus ?
	Genus ?
Rutaceae	*Zanthoxylum hordwellense* n. sp.
	Zanthoxylum compressum Chandler.
	Phellodendron costatum Chandler.
	Rutaspermum ornatum (Chandler).
Burseraceae	*Palaeobursera lakensis* Chandler.
Anacardiaceae	
Spondieae	Genus ?

Family	Genus and species
Icacinaceae	*Natsiatum eocenicum* Chandler.
	? *Iodes* sp. (or ? *Natsiatum* sp.).
	Iodes ? *hordwellensis* n. sp.
	Icacinicarya transversalis n. sp.
	Icacinicarya becktonensis n. sp.
Rhamnaceae	*Frangula hordwellensis* n. sp.
Sabiaceae	*Meliosma* sp.
Vitaceae	*Parthenocissus hordwellensis* n. sp.
	Vitis uncinata Chandler (V.20065).
	Ampelopsis rotundata Chandler.
	Tetrastigma lobata Chandler. (Decayed.)
Dilleniaceae	*Actinidia* sp.
Theaceae	
Theae	*Gordonia minima* Chandler.
	Gordonia truncata Chandler.
Taonabeae	*Eurya becktonensis* n. sp.
	Campylospermum hordwellense Chandler.
	Cleyera ? *stigmosa* (Ludwig).
	Anneslea ? *costata* n. sp.
	Hordwellia crassisperma (Chandler).
Thymeliaceae	Genus ?
Lythraceae	*Microdiptera parva* Chandler.
Cornaceae	
Mastixioideae	*Eomastixia rugosa* (Zenker).
	Mastixicarpum crassum Chandler.
	Mastixia ? *glandulosa* n. sp.
	Genus ?
Cornoideae	*Cornus quadrilocularis* Chandler.
	Dunstania glandulosa (Chandler).
Ericaceae	
Andromedeae	Genus ?
Rhododendroideae	Genus ? (Decayed.)
Epacridaceae	*Epacridicarpum headonense* Chandler.
Ebenaceae	*Diospyros headonensis* Chandler.
Symplocaceae	*Symplocos headonensis* Chandler.
	Symplocos sp.
Styracaceae	*Styrax elegans* Chandler.
Oleaceae	*Olea headonensis* n. sp.
Boraginaceae	*Omphalodes platycarpa* Chandler.
Acanthaceae	? *Acanthus* sp.
Caprifoliaceae	*Sambucus parvulus* Chandler.
Cucurbitaceae	*Cucurbitospermum reidii* n. sp.
Family ?	*Rhamnospermum bilobatum* Chandler.
	Carpolithus fibrosus n. sp.
	Carpolithus apocyniformis n. sp.
	Carpolithus sp. 8.
	Carpolithus sp. 6. (V.20107).
	Carpolithus sp. cf. *C. gardneri*
	Carpolithus sp. 1.
	Carpolithus spp.
	and tubers, rhizomes (V.20111 and V.40182–83 " *Nelumbium buchii* Ettingshausen "), placentas.

Paddy's Gap, Milford-on-Sea on the mainland. Wherever seen it is a conspicuous feature owing to a compacted mass of white shells—*Paludina*, *Melania* and fragments of *Unio*—which show up conspicuously the black dots due to crowded endocarps of *Limnocarpus* together with seeds of *Brasenia* and *Stratiotes*. The *Limnocarpus* Band is part of the Hordle Bed 31 of Tawney & Keeping.

A few specimens labelled *Limnocarpus* Band were collected at Colwell by James Groves with whom Clement Reid worked in the field while in retirement at Milford-on-Sea. A few others merely labelled Colwell Bay were in the Reid Collection. No distinctive Upper Headon fruits are among them and it therefore seems probable that these also were from the *Limnocarpus* Band.

A section given on pp. 132–133 of the Geological Survey Memoir on the Isle of Wight (1889) records a number of seams with lignite and seeds but experience suggests that these seeds were the usual *Brasenia*, *Stratiotes* and *Limnocarpus*. Nevertheless there is always a possibility that some rich pocket like those of Bed 10, Hordle, may someday reward persistent search. So far, however, despite the vigilance of Groves and Colenutt no such has been discovered in the Isle of Wight.

The short list of plants from the Lower Headon of Colwell is as follows:

Potamogeton pygmaeus Chandler
Limnocarpus forbesi (Gardner)
Stratiotes headonensis Chandler
Brasenia ovula (Brongniart)
Aldrovanda ovata (Chandler)
} all are water plants.

PTERIDOPHYTA

Order FILICALES

Family POLYPODIACEAE

Genus ***ACROSTICHUM*** Linnaeus

Acrostichum lanzaeanum (Visiani)

(Pl. 24, fig. 2)

1858. *Fortisia lanzaeana* Visiani, p. 431, pl. 1, fig. 8, pl. 2, figs. 1, 5.
1879. *Chrysodium lanzaeanum* (Vis.): Gardner & Ettingshausen, p. 26, pl. 2, figs, 3, 4.
1886. *Chrysodium lanzaeanum* (Vis.): Gardner, p. 402, pl. 3, fig. 5.
1925. *Acrostichum* (*Chrysodium*) *lanzaeanum* (Vis.): Chandler, p. 10.
1926. *Acrostichum lanzaeanum* (Vis.): Reid & Chandler, p. 33, pl. 1, figs. 4, 5.
Acrostichum lanzaeanum (Vis.): Chandler (in press), pl. 5, figs. 4, 5. Dorset Pipe-clay Series.

Reference to pinnules from Hordle was made by Chandler in 1925 and the first description, based on material in the Sedgwick Museum, Cambridge, was published by Reid & Chandler in 1926. In the British Museum there are seven further specimens (41420(5), V.42050–51) one of which shows no nervation so is doubtful and one showing the branching of the pinna. All are preserved in a carbonaceous grey clay and appear to come from Bed 10 below Hordle House.

Two fragments collected by H. Eliot Walton (V.42057–58) one of which showed also a seed of *Spirematospermum* (V.42057*a*) were alleged to come from the Barton Beds and a similar specimen, also collected by Walton, is in the Geological Survey Museum (7927). Mr. Walton was an amateur with no scientific training and the specimens may have been found loose on the foreshore. In view of the continuity of the Barton and Hordle sections the origin of this material requires confirmation by the finding of fresh pinnules at recognized Barton horizons. There is, however, no reason why the fern should not occur in the more estuarine Barton Beds for it persists from the Dorset Pipe-clay Series up to the Bembridge Series. A frond is shown (Pl. 24, fig. 2) for comparison with Hordle pinnules figured by Reid & Chandler, 1926 (see above).

Family SALVINIACEAE

Genus ***SALVINIA*** Adanson

Salvinia mildeana Goeppert

(Pl. 24, fig. 1)

1886. *Salvinia* sp. Gardner, p. 395.
1925. *Salvinia hantoniensis* Chandler, p. 10, pl. 1, fig. 1*a–d*; text-fig. 1.
1956. *Salvinia mildeana* Goeppert: Shaparenko, p. 30, pl. 1, figs. 1–3; text-fig. 9. Where earlier references to *S. mildeana* are given in full.

In a detailed study of the genus *Salvinia*, both living and fossil, Shaparenko (1956) has shown that the Hordle species should be referred to *S. mildeana*, a widespread form in the Tertiary of Europe from the Eocene to the Upper Miocene as shown by the list of fossil occurrences which he gives on p. 30. Material from Bed 10 below Hordle House is well represented in the British Museum. V.20010 and V.36341–46 include the specimens figured by Chandler (1925) and two unfigured specimens. V.36343 (Chandler, 1925, pl. 1, fig. 1*c*) also shows the counterpart of V.36342 (Chandler, 1925, pl. 1, fig. 1*b*) while V.36341 (Chandler, 1925, pl. 1, fig. 1*d*) shows the counterpart of V.36344 (Chandler, 1925, pl. 1, fig. 1*a*). V.36346 includes fourteen specimens from a single ironstone block found *in situ* two feet above the mammal bed in the foreshore. There are also nine blocks (V.43698), and one specimen (V.43699) in grey clay matrix.

GYMNOSPERMAE

Family PODOCARPACEAE

Genus ***PODOCARPUS*** (L'Hérit.)

? *Podocarpus* sp.

1883. *Podocarpus* sp. Gardner, p. 49, pl. 2, figs. 13, 14.

In a discussion under the heading *Podocarpus eocenica* Unger Gardner refers to two small coriaceous leaves from Hordle (spelt Hordwell) which he figures (V.15117–18). Another incomplete detached leaf impression is in the British Museum

(V.15119). Gardner comments of these leaves " if referable to *Podocarpus* " [they] " would probably belong to another species " [i.e. not to *P. eocenica* from Bournemouth which he was describing]. As the material is so doubtful and ill-preserved it is ignored in the plant list. The preservation suggests " Bed 10 " below Hordle House.

Family Taxodineae

Genus ***SEQUOIA*** Endlicher

Sequoia couttsiae Heer

The Hordle material is discussed and illustrated in detail in a forthcoming monograph on the Flora of the Dorset Pipe-clay Series (Chandler, in press) in which *Sequoia couttsiae* from all known Tertiary sites in the South of England is investigated. Hordle material is registered under the numbers V.20011–18, V.42052–53. It is particularly common in Bed 10 between Hordle House and Long Mead End and just east of Beckton Bunny ; it also occurs in the contemporary channel west of Long Mead End and is rare (V.20017) in the *Chara* Bed east of Long Mead End (Beds 27–29 of Tawney & Keeping).

ANGIOSPERMAE

Class MONOCOTYLEDONES

Family Potamogetonaceae

Genus ***POTAMOGETON*** Linnaeus

Potamogeton pygmaeus Chandler

(Pl. 24, figs. 3–6)

1925. *Potamogeton pygmaeus* Chandler, p. 13, pl. 1, fig. 3.
1926. *Potamogeton pygmaeus* Chandler : Reid & Chandler, p. 66, pl. 3, figs. 20–22.

The range has now been extended backwards into the Bournemouth Beds as will be described in a later monograph. Specimens have also been found in the *Limnocarpus* Band, Lower Headon, Colwell Bay, Isle of Wight (Pl. 24, figs. 3, 4). The holotype (V.20019) is in poor condition so a fruit impression (with counterpart V.17537) from the Bembridge Beds has been chosen as the neotype. It shows style and spines beautifully preserved (Reid & Chandler, 1926, pl. 3, fig. 20). There are about fourteen other specimens from Hordle which show spine bases, some having the valve preserved (V.20020–20*a*, V.42056). They are from Bed 10 east of Beckton Bunny. P. I. Dorofeev considers (*ex lit*) that the nearest living affinity is with the North American *Potamogeton spirillus* Tuckerm.

Genus ***LIMNOCARPUS*** Reid emend. Reid & Chandler, 1926 : 68

Limnocarpus forbesi (Heer)

(Pl. 24, figs. 7–11)

For synonyms and references see Chandler, 1961*a*, p. 28.

The species formerly designated *L. headonensis* (Gardner) must now be referred to *L. forbesi* (Heer) for reasons explained by Chandler (1961*a* : 28). Endocarps are extremely abundant at certain horizons in the Lower Headon Beds at Hordle, notably in the Crocodile Beds between Hordle House and Long Mead End (Bed 15 of Tawney & Keeping) and in the *Limnocarpus* Band formerly peculiarly well displayed at Paddy's Gap, Milford-on-Sea. Figured specimens still extant are V.20021 (Chandler, 1925, pl. 1, fig. 4*a*) and V.20022*b* (Chandler, 1925, pl. 1, fig. 4*b*). The originals of Chandler, 1925, pl. 1, fig. 4*c* and text-fig. 3 have decayed but V.20023 still shows five endocarps split longitudinally through the funicle and placenta as in the text-figure. Other specimens from Hordle are V.20022*a*, *c*, V.20024–27 (including four paired endocarps), V.20028–30, V.31789, V.42059–60.

Endocarps (V.42062–63) were also found in a bomb crater at 50 ft. O.D. on the east side of the Dane stream, Downton, Hordle. The crater showed about 5 ft. of white micaceous sand like the *Unio* sands of Paddy's Gap, Hordle cliff, and below were 10 ft. of greenish clay with a band of *Limnocarpus* 6 ft. down.

At Colwell Bay, Isle of Wight, Groves collected numerous specimens (V.42064–67) in the *Limnocarpus* Band (exact site unspecified) and Chandler obtained others (V.42068) at the same horizon below Warden Battery.

Family HYDROCHARITACEAE

Genus ***STRATIOTES*** Linnaeus

Stratiotes headonensis Chandler

(Pl. 24, fig. 17)

1923. *Stratiotes headonensis* Chandler, p. 117, pl. 5, figs. 1–3, 24–26 ; pl. 6, fig. 23.
1925. *Stratiotes headonensis* Chandler : Chandler, p. 14.
1960. *Stratiotes headonensis* Chandler : Chandler, p. 223, pl. 33, figs. 96, 97.

A full description of the species was given in 1923. For convenience of comparison with *S. hantonensis* a diagnosis is given : Seed oblong, ovate or subtrigonal, somewhat flattened, hooked at the base. Keel often from one-third to one-half the breadth of the seed. Collar small, conspicuous, usually warty. Testa thick, woody with marked longitudinal ridges. Micropyle basal or subbasal, usually oblique. Hilum basilateral, raphe marginal or submarginal almost to the apex. Cells of internal surface of keel much contorted. Length of seed from about 3·25 to 6·5 mm. ; breadth about 2·25 to 4 mm.

REMARKS. The following were figured by Chandler, 1923, pl. 5, fig. 1 (V.40068), pl. 5, fig. 2 (V.40067*a*), pl. 5, fig. 24 (V. 40066). The species is very abundant in

Bed 10, 49438, V.13567, V.16538, V.20031–32, V.31788, V.40067–68*a*, V.42073, V.42078 (precise position in the cliff unspecified), V.42069 (east of Beckton Bunny), V.42070 (below Hordle House). Also very abundant in Bed 31 at Paddy's Gap (V.42066, V.42071). It occurs sparsely in Bed 29 between Hordle House and Milford Corner (V.42072). Horizon in Lower Headon Hordle unspecified in V.16537–38*a*.

It is equally abundant at Colwell Bay, V.42076 (Chandler, 1923, pl. 5, fig. 3), V.42077, V.42079–81, all presumed Lower Headon, and V.42074 *Limnocarpus* Band, site unspecified, V.42075 same band below Warden Battery.

The oldest record of the species up to date is at Horizon L. of the Barton Series, Barton cliff (Chandler, 1960 : 223).

Stratiotes hantonensis Chandler

(Pl. 24, figs. 12–16)

1960. *Stratiotes hantonensis* Chandler, pp. 205, 222, pl. 30, figs. 18–25 ; pl. 33, figs. 87–95.

The description given in 1960 applies equally to the seeds from the Lower Headon Beds. Typical measurements of Hordle material are 2·6 by 1·6 mm. ; 2·8 by 1·2 mm. ; 3 by 1·6 mm. ; 3 by 1·5 mm. The thickness of the seeds is about 1·3 mm. This small species was overlooked when *S. headonensis* was described in 1923, its tiny seeds being merely regarded as small immature examples of *S. headonensis*, only about sixteen specimens (V.42082–86*a*) were found. Now that *S. hantonensis* has been collected in large numbers in older beds ranging from Bournemouth through the Hengistbury Beds, Highcliff Sands and Barton Beds its distinctive characters are well known and it was no longer confused with *S. headonensis* when the Hordle seeds were re-examined. The range of the two species therefore overlaps at the western end of the Hordle section. So far only gatherings of *S. headonensis* from Bed 10 close to Beckton Bunny have yielded *S. hantonensis*. The absence from older deposits of typical *S. headonensis* with its broad flat keel, coarse pitting, pronounced ridges and larger size in association with *S. hantonensis* confirms that the latter is a distinct species.

Family CYPERACEAE

Genus ***CARICOIDEA*** Chandler, 1957 : 86

Caricoidea minima (Chandler)

(Pl. 24, figs. 18–21)

1925. *Cladium minimum* Chandler, p. 14, pl. 1, fig. 5*a*, *b*.
Caricoidea minima (Chandler) Chandler (in press), pl. 7, fig. 1.

DIAGNOSIS. Fruit sub-obovoid sometimes slightly flattened laterally, rather abruptly narrowed to the apex, truncate at the base. Fruit wall thick, epidermis of digitate rectangular cells. Length about 2·75 to 3 mm. ; maximum diameter, 2 to 2·5 mm. Endocarp oburceolate with short truncate basal neck, rounded or pointed apex. Wall of two layers the inner columnar in section, formed inside and out of conspicuous equiaxial cells. Length, 1·25 to 1·65 mm.; breadth, 1 to 1·55 mm. Seed with testa of transversely elongate cells.

HOLOTYPE. Brit. Mus. (N.H.), No. V.20033.

DESCRIPTION. *Fruit:* Sub-obovoid, sometimes slightly flattened laterally, truncate at the base which has a short canal with large foramen marking the attachment. Somewhat pointed at the apex, not conspicuously attenuated or mucronate but abruptly narrowed. Epidermis shining of digitate cells usually more or less rectangular and somewhat longitudinally elongate and aligned, their width about 0·012 to 0·016 mm. Wall thick, spongy, formed of a mass of equiaxial cells about 0·01 mm. in diameter. Length of fruit, 2·75 to 3 mm.; maximum diameter, 2 to 2·5 mm.

Endocarp: More or less oburceolate but contracted rather abruptly as a rule to form a short truncate basal neck pierced by a canal, rounded or pointed at the apex, sometimes with two or three external strands of longitudinal fibres. Wall thick, compact tending in fossilization to separate into two layers, an outer compact close-textured layer about 0·15 mm. thick and an inner layer, columnar in section, about 0·037 mm. thick formed superficially inside and out of equiaxial cells about 0·016 mm. in diameter. Length of endocarp about 1·25 to 1·65 mm.; breadth, 1 to 1·55 mm.

Seed: Represented by testa formed of transversely elongate cells arranged in rows.

REMARKS. Detached endocarps (V. 20033, V.20033*a*) were described as *Cladium minimum* before fruits had been seen (Chandler, 1925: 14, pl. 1, fig. 5*a*, *b*). Fruits from Bed 10 (V.42087–88, V.42091) and additional endocarps (V.42089–90) have now been found. Four crushed endocarps have also been recognized from Bed 29 in the lignitic bands (V.20047*b*). While relationship is certainly with the Caricoideae the fruit characters show that these specimens differ from *Cladium* itself which has a thin spongy fruit wall and an epidermis of large rectangular smooth-walled cells. The fossils are therefore referred to the form-genus *Caricoidea* pending the discovery of further evidence. A fruit has now been found in the Dorset Pipe-clay Series at Arne.

Caricoidea obscura Chandler

(Pl. 24, figs. 22–24)

1960. *Caricoidea obscura* Chandler, pp. 207, 223, pl. 30, figs. 27–33; pl. 33, figs. 98–105.
Caricoidea obscura Chandler: Chandler (in press), pl. 6, figs. 20–33.
1961*a*. *Caricoidea obscura* Chandler: Chandler, p. 33, pl. 7, fig. 34.

DESCRIPTION. *Fruit:* As described from Hengistbury (p. 207 quoted above). The single fruit seen from Hordle has a somewhat three-sided basal truncation and is itself obscurely three-sided one side being broader and flatter than the other two. Epicarp although poorly preserved shows the finely digitate cell walls about 0·016 mm. broad. Beneath the epicarp the equiaxial cells of the spongy tissue are about 0·01 mm. in diameter and light brown in colour. Length about 1·75 mm.; breadth, 1·5 mm.

Endocarp : Also as described. One or more longitudinal ridges arise at the base and gradually die out on the body of the endocarp but these are not always present. Surface smooth externally and the spongy wall, about 0·07 mm. thick, is formed of equiaxial cells. Dimensions of several endocarps are : 1 by 0·8 mm. ; 0·9 by 0·75 mm. ; 1·15 by 0·85 mm. ; 1 by 0·7 mm. ; 0·9 by 0·9 mm.

Seed : Poorly preserved represented only by much decayed adherent testa formed of transversely elongate cells which produce striae about 0·012 mm. apart.

REMARKS. About a dozen endocarps were found (V.42095) in addition to the figured material. The species is based on well preserved fruits and endocarps from the Highcliff Sands near Mudeford and the Dorset Pipe-clay Series and also awaits description from the Bournemouth Freshwater Beds. Specimens have been described from the Upper Hengistbury and Lower Barton Beds (Chandler, 1960).

Genus ***SCLERIA*** Berg.

Scleria hordwellensis n. sp.

(Pl. 24, figs. 25, 26)

DIAGNOSIS. Fruit subglobular, mucronate at the apex, flattened at the base and seated on a rounded triangular thick disc with transversely puckered surface. Surface of fruit smooth but with slight longitudinal fluting on the sides. Surface of both fruit and disc of equiaxial cells. Length of fruit with mucro and disc, 1·75 mm. ; breadth, 1·75 mm.

HOLOTYPE. Brit. Mus. (N.H.), No. V.42096.

DESCRIPTION. *Fruit :* Subglobular with short thick apical mucro. Base somewhat flattened pierced by an aperture but without a narrow neck like that of *Cladium* and *Mapania*. Circumference of fruit rounded not triangular. Sides slightly grooved or fluted longitudinally, seated when found on a thick rounded triangular disc which still adheres on one side but is elsewhere now broken. Its removal has shown a rounded triangular scar at the base of the fruit itself about 1·3 mm. in diameter. The angles of the disc originally extended half way up the fruit. Its surface is rippled or puckered transversely. Epidermis of fruit and disc formed of equiaxial cells, many about 0·008 mm. in diameter. Inside the disc as shown along the broken edge are equiaxial cells, 0·016 mm. in diameter. Length of fruit with disc and mucro, 1·75 mm. ; breadth, 1·75 mm.

REMARKS AND AFFINITIES. One fruit which suggests relationship to *Scleria* of the type *S. laevis*. The genus occurs in all tropical and subtropical regions with a single species in Atlantic North America.

Family CYPERACEAE, Genus ?

(Pl. 24, fig. 27)

A fruit (V.42097) too poorly preserved for generic determination. Suboval in outline, shortly stipitate with acuminate apical style. Probably originally inflated but somewhat compressed in fossilization. Surface with regular equiaxial cells about 0·025 mm. in diameter with raised walls (these possibly due to differential decay). Length of fruit, 1·45 mm. ; breadth, 1 mm.

Family ZINGIBERACEAE

Genus *SPIREMATOSPERMUM* Chandler, 1925 : 17

Spirematospermum headonense n. sp.

(Pl. 24, figs. 28–30 ; Pl. 25, figs. 31, 32)

1925. *Spirematospermum wetzleri* (Heer) : Chandler, p. 17, pl. 1, fig. 8*a–c* ; text-fig. 5.

DIAGNOSIS. *Fruit :* Bisymmetric with rounded upper surface and sharply angled lower margin hence obovoid in transverse section. Estimated length probably less than 25 mm.; maximum transverse diameter, 7 to 9 mm. Thickness of fruit wall, 0·228 mm. (maximum). Number of seeds in fruit probably not more than twelve arranged in one or two rows on parietal placentas in the plane of symmetry. Locules one ? or two ? Length of seeds, 6·25 to 7·25 mm. ; maximum breadth, 1·5 to 2·25 mm. All tissues of seeds spirally arranged in relation to the seed cavity.

HOLOTYPE. Brit. Mus. (N.H.), No. V.42098.

DESCRIPTION. *Fruit :* Inferior, bisymmetric, many-seeded, the maximum number of seeds estimated to be not more than twelve, eight actually counted in the holotype. Truncate lanceolate, the apex bearing a flat elliptical superior perianth disc (V.42100 Chandler, 1925, text-fig. 5 (4)). Base narrowing gradually into a thin curved stalk (V. 42098–99). Upper margin rounded, lower sharply angled in the plane of symmetry the angle being continued along the stalk, so that clearly it is an original feature ; hence in transverse section the fruit is obovoid. External surface ornamented with longitudinal ribs due to fibres within the wall. Whole surface covered by square or hexagonal cells from 0·027 to 0·055 mm. broad, arranged more or less regularly in longitudinal rows. Cell walls thin, possibly the cells were much inflated in life and have collapsed. Thickness of fruit wall now 0·055 to 0·228 mm. at most. Even supposing that the wall has been thinned by collapse of the cells on drying the maximum original thickness can scarcely have exceeded 0·35 mm. (contrast *S. wetzleri* (Heer) from the German Brown Coal 3 to 6 mm. thick). Number of locules cannot be verified in the absence of new and better material, although it should be borne in mind that the supposed septum may have been inner layers of fruit wall separated by maceration. Seeds arranged in one or two rows on parietal placentas in the plane of symmetry. (*S. wetzleri* one-loculed with three parietal placentas and six rows of seeds.) Although no fruits are complete it is estimated that not more than a dozen seeds can have been enclosed by these small fruits. Eight are preserved in the holotype (numerous seeds in excess of twelve are shown in the figures of *S. wetzleri*). Dehiscence by irregular fracture or dissolution of the fruit wall. Estimated length of fruit not less than 20 or more than 25 mm. Maximum diameter, 7 to 9 mm. (*S. wetzleri* 25 to 100 mm. in length. Maximum diameter, 30 mm.)

Seed : (V.20037–38*a*, V.42101) Anatropous ; varying in shape through mutual pressure in the pod, hence frequently somewhat facetted, elongate, often sub-cylindrical, apex rounded or pointed, base truncate directed towards the apex of the fruit. Base with a funnel-shaped depression which encloses the hilum, a lateral opening leading into the lateral raphe canal which traverses the thick testa to the subapical chalaza (Chandler, 1925, text-fig. 5 (1)). At the base of the depression is the circular micropylar opening into the seed cavity. In well preserved specimens it is closed by a thin circular plug with central external mucro. The raphe opens into a small apical cavity at the extremity of the flask-shaped seed cavity and the chalaza is situated where the two cavities are adjacent.

The testa is thick and in all layers the cells are arranged spirally around the seed cavity, an arrangement apparent in weathered or dissected specimens but not seen in a freshly sectioned surface or thin section. The epidermis is smooth and shining externally with spiral striae, deeper striae alternating with four or five slighter ones. The cells which form this surface are very long and narrow as described by Kirchheimer for *S. wetzleri* but in sections of the seed they produce a coarsely columnar effect. Within the epidermis in longitudinal sections of the seed two closely fused thick layers are distinguishable. The outer of these, about 0·11 mm. thick in one seed measured, shows small equiaxial cells (secreting ? or endosperm cells ?). They represent the transverse diameters of spirally arranged cells (in *S. wetzleri* this outer layer has tangentially elongate cells as seen in section). The inner layer is 0·275 to 0·33 mm. thick and the cells, in section equiaxial, are larger than those of the outer layer. A thin cuticle lines the seed cavity which is formed of hexagonal cells, 0·018 mm. in diameter. The spiral arrangement of the inner layers is clearly seen impressed on the lining of the seed cavity. Length of seeds, 6·25 to 7·25 mm. ; diameter, 1·5 to 2·25 mm. (*S. wetzleri* length, 5 to 10·2 mm. ; diameter up to 5 mm.).

REMARKS. Fruits and seeds were formerly obtainable in Bed 10 below Hordle House and it appears fairly certain that the holotype was from this site where Mr. & Mrs. Clement Reid were in the habit of collecting. Seeds were rare in Beds 27–29 (V.20038). A seed embedded in a mass of *Acrostichum* (V.42057*a*) was alleged to be from Barton but see comment on p. 102.

In 1936 and again in 1957 the structure of *Spirematospermum wetzleri* (Heer) from the German Brown Coal was fully described by Kirchheimer. Much help in interpreting details of structure in the Headon material was obtained from his work. The existing condition of Hordle cliff makes it impossible to find new material for further study and this is unfortunate as only three fruits (all imperfect) and a number of isolated seeds are known. All the fruits show consistent characters which now seem to distinguish them from the typical Brown Coal *S. wetzleri*. These distinctive characters are indicated in the above description by introducing the corresponding features of *S. wetzleri* in brackets. There seems to be no doubt that the bisymmetry of the Hordle fossils is original and the fruits were never round in transverse section. The almost papery thin walls are unlikely through shrinkage on drying to have been derived from walls 3 to 6 mm. thick like those of *S. wetzleri*. The number of locules cannot finally be settled at present. However apart from this doubtful character the shape, size and thickness of the German fruits, the larger number of seeds, and the size of these seeds seem sufficient ground for separating the specimens from Hordle as a distinct species, *S. headonense*.

Kirchheimer is in agreement that the genus *Spirematospermum* is an extinct member of the family Zingiberaceae.

The figures and description of *Spirematospermum* from the Bovey Tracey Lignite, Devon, give insufficient evidence as to the species which has therefore been retained in *S. wetzleri* as originally described. The small size of the isolated seeds from Bembridge suggests that these should possibly be redesignated *S. headonense* although they fall within the range of size of the Oligocene *S. wetzleri*.

Class DICOTYLEDONES

Family Myricaceae

Genus ***MYRICA*** Linnaeus

Myrica boveyana (Heer) pars

(Pl. 25, figs. 33, 34)

1862. *Carpolithes boveyanes* Heer, p. 1077, pl. 70, ? figs. 7–14 (in part).
1957. *Myrica boveyana* (Heer) pars : Chandler, p. 90, pl. 12, figs. 45–48.
1961. *Myrica boveyana* (Heer) pars : Chandler, p. 328, pl. 33, figs. 1–4.

Description. *Endocarp :* One-loculed, bisymmetric, splitting into equal valves. Valves more or less oval in outline, somewhat inflated. External surface so much abraded as to show little structure but a few obscure rather irregular longitudinal furrows for fibres. Locule suburceolate, not nearly as deep as broad, narrowing above into the apical stylar canal. Wall pierced at the base by a short straight canal for the funicle. Marginal sutures wide, smooth, flat, close-textured, broadest at about a quarter of the length from the apex where they may be 0·6 to 0·7 mm. wide. These wide sutures tend to produce a slight marginal flange on the outer surface which appears to break readily owing to its thinness as shown in one specimen. At the base of the endocarp the suture is narrower and only about 0·2 mm. wide. Seed not preserved. Length of endocarp, 2·75 mm. ; maximum breadth, 2·5 mm.

Remarks. Two valves from different endocarps. Although so abraded and sand-pitted that the cell structure is obscure, they appear to be indistinguishable from *M. boveyana* (Heer) from the Oligocene Lake Basin of Bovey Tracey, Devon, and from the London Clay of Nursling, Southampton, judging by size, proportions and locule shape.

Family Betulaceae

Genus ***CARPINUS*** Linnaeus

Carpinus boveyanus (Heer)

(Pl. 25, fig. 35)

1862. *Carpolithes boveyanus* Heer, p. 1077, pl. 70, figs. 7–14 (in part).
1957. *Carpinus boveyanus* (Heer) pars : Chandler, p. 92, pl. 13, figs. 52–67.

Description. *Fruit :* Pointed-ovate in outline, bisymmetric, much compressed with large basal scar of attachment of which half is on each face. Surface covered by an accrescent calyx. Longitudinal furrows arise at the margin of the scar; three can be seen on one face, four on the other but owing to abrasion they become obscure in places, some being entirely obliterated. The vascular strands they once contained are not preserved. External surface finely striae, the striae formed by elongate cells about 0·009 to 0·012 mm. broad. Beneath this surface and partly exposed by abrasion are equiaxial cells about 0·025 mm. in diameter. Length of fruit, 2·8 mm.; breadth, 2·25 mm.; thickness, 0·75 mm. Diameter of basal scar, 1 mm.; height measured on one surface, 0·25 mm.

REMARKS AND AFFINITIES. One fruit with accrescent calyx preserved but no bract. Comparison with fruits from the Bournemouth Marine Beds at Southbourne, the Highcliff Sands (both awaiting publication) and the Bovey Tracey Beds, Devon, indicate that a single species occurs at all these localities.

Family MORACEAE

Genus **BROUSSONETIA** L'Hérit.

Broussonetia rugosa Chandler

(Pl. 25, figs. 36, 37)

1925. *Broussonetia rugosa* Chandler, p. 21, pl. 3, fig. 1*a*, *b*.

DIAGNOSIS. Endocarp suboval in outline with knob-like projection carrying stylar canal and funicular opening, bisymmetric, somewhat compressed at right angles to plane of symmetry. Surface finely pitted, ornamented with elongate tubercles with sinuous outlines. Thick inner part of wall columnar. Dimensions: 1·75 by 1·4 mm.; 1·25 by 1 mm.

DESCRIPTION. *Endocarp:* Suboval in outline, with knoblike projection at one end, bisymmetric, somewhat compressed at right angles to the plane of symmetry with broad surfaces gently convex. Stylar canal and funicular canal adjacent on the projection. Endocarp splitting marginally for germination, having a single pendulous seed. External surface ornamented with elongate tubercles having irregular sometimes sinuous outlines. The tubercles radiate from the stylar projection. Whole surface finely pitted. Thickness of wall about 0·1 mm., seen in section to be formed of an outer thin compact layer and an inner thick layer of columnar cells. Diameters of two endocarps in plane of symmetry: 1·75 by 1·4 mm. and 1·25 by 1 mm.

REMARKS. In addition to the two figured specimens there are three fragments (V.20039*a*). The projection at one end of the endocarp is seen in living material of *Broussonetia* and *Morus* to taper into the funicle but in the fossils the funicle itself is gone and only the worn down process remains. The fossils resemble *Ficus* in size and form but no rugose species of *Ficus* has been seen whereas in *Broussonetia* all the characters described are present.

Section MOROIDEAE

Genus ***MOROIDEA*** Chandler, 1957 : 95

Moroidea hordwellensis n. sp.

(Pl. 25, fig. 38 ; Text-fig. 1)

DIAGNOSIS. Fruit more symmetric than *M. boveyana*, with broad flat stylar projection and canal. Dimensions in plane of symmetry : 1·7 by 1·5 mm.

HOLOTYPE. Brit. Mus. (N.H.), No. V.42105.

DESCRIPTION. *Fruit :* Bisymmetric, subcircular in outline, cuneate in transverse section, the narrow edge crested for nearly half the circumference and the opposite edge rounded. Style and funicle close together each marked by a conspicuous marginal prominence. The stylar prominence is broad, flattened terminal on the crested margin and pierced by a flat canal 0·1 mm. broad ; the attachment or funicular prominence is recurved away from that of the style, subapical, terminal on the rounded margin. Pericarp 0·1 mm. thick along the crest, 0·05 mm. thick on the rounded margin, hard, woody formed of compact parenchyma, the cells on the external surface measuring about 0·012 to 0·016 mm. in diameter and in sections of the wall showing a radial alignment. Locule lining of approximately hexagonal cells about 0·025 mm. broad and 0·05 mm. long, their longer axes diverging from the placental region giving rise to obscure divergent striae. Dehiscence occurs along the crested margin. Seed solitary, pendulous from the subapical placenta which immediately underlies the funicular prominence, the funicle being short and thick. Dimensions of fruit in plane of symmetry, 1·7 by 1·5 mm. ; thickness at right angles to plane of symmetry, 1 mm. Length of funicular prominence, 0·17 mm.

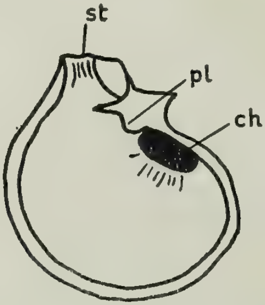

FIG. 1. *Moroidea hordwellensis* n. sp. Longitudinal section through fruit and seed. (*st*) stylar prominence, (*pl*) placenta, (*ch*) chalaza on closely adherent seed within fruit. ×21 approx.

Seed : Campylotropous, chalaza conspicuous, subcircular, 1·2 mm. in maximum diameter contiguous with the hilum but on the far side of it from the style as the seed is seen lying within the fruit. Testa brittle, only 0·025 mm. thick tending to adhere to the locule, formed of small equiaxial cells 0·012 to 0·016 mm. in diameter near the hilum where best preserved. Inner surface of testa with elongate cells about 0·025 mm. broad, having cell walls represented by a double line.

Remarks and affinities. One fruit slightly broken near the crested margin and, on one surface, near the attachment. The broken surface was subsequently removed and the remains of a seed exposed. Only the hilar end of the seed was preserved but it showed the perfect chalaza scar.

Form and structure indicate Moraceae and probably the section Moroideae (Engler) or the Artocarpoideae in both of which the seeds may be campylotropous and the chalaza in the position described. On the whole the Moroideae appear to bear the closer resemblance to the fossil. A species distinguished by a narrower stylar prominence and canal and greater asymmetry was described from Bovey Tracey under the name *Moroidea boveyana* Chandler (1957 : 95, pl. 13, fig. 74).

Genus ***BECKTONIA*** nov.

Diagnosis. One-loculed one-seeded endocarps referable to Moraceae, roundly triangular at apex the angles alternating with more or less flattened sides, rounded below, with oblique apical foramen and placenta subjacent to it. Length, 3·3 to 4·25 mm. ; breadth, 2·4 to 3·5 mm. (compressed).

Type Species. *Becktonia hantonensis* n. sp.

Becktonia hantonensis n. sp.

(Pl. 25, fig. 39)

Diagnosis. That of the genus.

Holotype. Brit. Mus. (N.H.), No. V.42106.

Description. *Endocarp :* Subovoid, roundly triangular above, rounded below, the rounded apical angles dying out gradually but subsidiary intermediate ridges occurring in the lower part. Foramen for funicle subapical oblique. Surface rather rough formed of fine equiaxial cells 0·007 to 0·008 mm. in diameter. Wall about 0·15 mm. thick, close textured in section, carbonized so that cell structure is obscure but a radial or columnar alignment can be detected. Length, 4·25 mm. ; breadth (reduced by contraction), 2 mm.

Remarks and affinities. An endocarp bursting below. The specimen is identical with endocarps from the Bournemouth Freshwater Beds awaiting publication. These endocarps range in length from 3·3 to 3·5 mm. ; breadth, 2·4 to 2·75 mm.

The single seeded locule with hard endocarp, locule lining with digitate cells (seen in the Bournemouth specimens), oblique funicular aperture and pendulous anatropous seed (also seen in Bournemouth specimens) indicate the family Moraceae.

Order CENTROSPERMAE

Family CARYOPHYLLACEAE

Genus ***HANTSIA*** Chandler, 1960 : 209

Hantsia pulchra (Chandler)

(Pl. 25, fig. 40 ; Text-fig. 2)

1925. *Corydalis pulchra* Chandler, p. 25, pl. 3, fig. 10*a*, *b*.
1929. *Corydalis pulchra* Chandler : Reid & Chandler, pl. 1, fig. 18.
1960. *Hantsia pulchra* (Chandler) Chandler, p. 209, pl. 31, fig. 39.

DESCRIPTION. *Seed :* Obliquely or transversely oboval or subcircular in outline, much compressed laterally, bisymmetric about a plane passing through hilum and micropyle. Seed cavity undivided by any partition between the limbs of the large curved embryo of which the radicular limb is longer and narrower than the other. The embryo may have occupied the whole seed cavity or have been surrounded by only a thin film of endosperm as is suggested by the surface contours (cf. Pl. 25, fig. 40). Hilum a large oval or subcircular gaping aperture between the tips of the limbs with smooth raised rim and cells with straight walls. Testa formed of two coats, the outer 0·1 to 0·15 mm. thick, black and shining, closely and conspicuously tubercled, the tubercles being dome-shaped and subcircular in outline except around the margin and over the micropylar limb where they tend to be elongate parallel with the margin. Each tubercle arises from a single " cell " or area with finely toothed outline, the teeth measuring about 0·02 mm. in breadth, the diameter of the tubercled areas being about 0·07 to 0·1 mm. The teeth are frequently but not invariably difficult to see in surface view but are clear on broken edges where they produce a columnar effect on account of the rounded ridges they form on the sides of the cells. The testa readily cracks along these toothed outlines. The tubercled areas sometimes break down and then appear to be formed of small equiaxial cells 0·016 to 0·025 mm. in diameter. An inner black coat, 0·016 mm. thick where measured, may become partly separated in fossilization from the outer

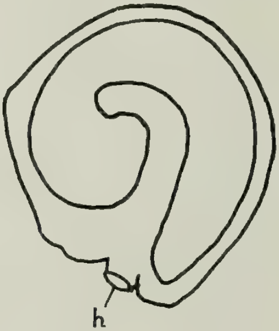

FIG. 2. *Hantsia pulchra* (Chandler). Longitudinal section through a seed showing large embryo (inferred) and large hilar opening (*h*) between limbs. × 15.

coat. Its surface is close textured formed of equiaxial cells about 0·015 mm. in diameter. Tegmen light brown, semitranslucent, of straight-sided angular cells about 0·012 to 0·015 mm. in diameter, rough. Dimensions of typical seeds are: 1) Length along axis between limbs, 2 mm.; breadth across both limbs, 2·5 mm. 2) Length, 2·25 mm.; breadth, 1·75 mm.

REMARKS. The species was originally referred to the genus *Corydalis* but fuller information now available suggests that the affinities need revision. Fine teeth around the tubercled surface cells (or areas) were originally overlooked but have now been clearly seen. No such digitate cells occur in *Corydalis* where the walls of the tubercled areas are straight and smooth. Again in *Corydalis* the tegmen is thin and diaphanous adhering closely to the outer coat and is formed of large irregular cells which vary in size from 0·016 by 0·05 mm. to 0·012 by 0·08 mm. This in no way resembles the tegmen of the fossil with its small uniform equiaxial cells. Further search was therefore made in the order Centrospermae which has large curved embryos occupying the circumference of the seed. Among the Chenopodiaceae *Beta* shows superficially similar cells but these are smooth walled not digitate; its tegmen is similar to that of the fossil. Portulacaceae, with digitate cells, is excluded by the form of the seed. In Caryophyllaceae the tubercles are always finely digitate while in *Saponaria* they may be similar in appearance and distribution. Again the limbs of the curved seed may be unequal as in the fossil but there is no conspicuous hilar rim projecting between them although the tegmen is formed of small equiaxial cells. In *Silene* a hilar rim occurs but shows distinct digitate cells on its surface and the testa cells are radially aligned the limbs of the seed being more or less symmetrical. No living genus seen shows all the characters described but as they do occur within the family Caryophyllaceae the nearest relationship is presumed to lie here. The generic name indicates the geographical origin of all specimens to date. In addition to the figured material there are a number of broken or incomplete seeds (V.42108–09) some of which show important characters.

Hantsia glabra n. sp.

(Pl. 25, figs. 41–43)

DIAGNOSIS. Resembling *H. pulchra* except in the smooth surface, the digitate cells being flat or scarcely convex, not markedly tubercled. Dimensions of best developed seed: 2·3 by 2 mm.

HOLOTYPE. Brit. Mus. (N.H.), No. V.42111.

DESCRIPTION. *Seed:* Subcircular or transversely obovai in outline, much compressed laterally, bisymmetric about a plane passing through hilum and micropyle, embryo curved with unequal limbs the micropylar limb longer and narrower than the other. Seed cavity not divided by a partition between the limbs. Hilum a large oval or subcircular gaping aperture between the limbs or almost terminal on the narrower limb surrounded by smooth upstanding rim as in *Hantsia pulchra*. Testa black and shining formed of cells which are subcircular or oval in outline with finely toothed margins having from about nine to fifteen small teeth. The surface of these cells is flat or very slightly convex not tubercled as in *H. pulchra*. The testa has a marked tendency to break along the toothed outline of the cells. Surface of cells finely granular. Size of cells varying from about 0·075 to 0·1 mm. in diameter but on the tip of the micropylar limb they are much smaller and some at least are straight-sided not toothed. Along the circumference of the seed they tend to be elongate and narrower. These toothed cells show clearly on the inner surface of the testa which is about 0·05 mm. thick. There are traces of a thin light brown inner coat (tegmen?) not clearly seen. The manner in which the cells of the outer coat break up suggests that they may be formed of groups of smaller equiaxial cells which perhaps give rise to the granular appearance. Greatest diameter of seed measured across two limbs, 2·3 mm. ; greatest diameter at right angles to this in plane of symmetry, 2 mm. ; thickness at right angles to plane of symmetry, 0·4 mm. Hilar aperture including thickness of wall, 0·1 by 0·15 mm. A second seed is distorted so does not give correct measurements but may have been somewhat smaller.

REMARKS. Obviously related to *Hantsia pulchra* which it closely resembles in everything but its smooth surface and in the apparent absence of an inner coat of the testa formed of small equiaxial cells. The possibility that both may belong to a single species with some smooth and some tubercled seeds as in Caryophyllaceae and Fumariaceae cannot be excluded, but the difference in the fossils is so pronounced that pending further discovery as to closer relationship it appears best to regard them as distinct.

In this as in *H. pulchra* a depressed area between the limbs on the broad surfaces suggests a large embryo, probably with little albumen, having a conspicuous large radicle and broad cotyledonary limb.

Family NYMPHAEACEAE

Genus ***BRASENIA*** Schreber

Brasenia ovula (Brongniart)

1926. *Brasenia ovula* (Brongn.) : Reid & Chandler, p. 99, pl. 6, figs. 15–18 (see for earlier references).
1957. *Brasenia ovula* (Brongn.) : Chandler, p. 96, pl. 13, fig. 75.
1960. *Brasenia ovula* (Brongn.) : Chandler, pp. 210, 224, pl. 31, figs. 40, 41 ; pl. 33, figs. 106, 107.

Seeds abound in the Lower Headon both at Hordle and Colwell Bay, certain horizons being blackened by their shining testas. At Hordle they are especially abundant in Beds 9 and 10 below Hordle House (V.20045–46, V.20048, V.42112–14 embryotegas) and just east of Beckton Bunny (V.42115), Bed. 29 (V.20047) and Bed 31 (V.20044). Site in Bed 10 unspecified (V.31790). At Colwell Bay a number of seeds collected by Clement Reid are presumed to come from the Lower Headon (V.42116–18). Those by J. Groves (V.42119) are from the *Limnocarpus* Band and those by Chandler (V.42120) from this same horizon below Warden Battery.

Brasenia spinosa Chandler

1925. *Brasenia spinosa* Chandler, p. 22, pl. 3, fig. 4; text-fig. 7.
1925. *Brasenia antiqua* Chandler, p. 22, pl. 3, fig. 5*a*, *b*.

DIAGNOSIS. Seed globular or ovoid, raphe ridge inconspicuous. Surface with faint longitudinal ridges and slender spiney tubercles or broad, short or wart-like tubercles especially abundant over the chalazal end of the seed. Surface of interlocking digitate cells. Embryotega circular or elliptical with central rimmed micropyle and oblong or square convex surface cells with finely toothed margins. Tegmen semitranslucent of equiaxial angular frequently hexagonal thin-walled cells. Length of seed, 1 to 2·6 mm.; breadth, 0·8 to 2 mm., exceptionally 2·5 mm.

HOLOTYPE. Brit. Mus. (N.H.), No. V.20041*a* originally regarded as a distinct species named *Brasenia antiqua*. The original and only seed of *B. spinosa* now decayed.

DESCRIPTION. *Seed:* Globular or ovoid, anatropous, with inconspicuous longitudinal raphe ridge, hilum obscure where the ridge terminates against the embryotega. Surface with faint rounded longitudinal ridges, sometimes ornamented with slender spines or tubercles, sometimes with shorter, thicker, blunt or wart-like tubercles. The tubercles are usually most abundant over the chalazal end of the seed. The rounded ridges frequently correspond with the rows of cells which form the testa. The cells which may be about 0·05 to 0·1 mm. in diameter are digitate some having as many as ten digitations, others only six to eight; these may be arranged in three or four pairs. Each tubercle or spine arises from the centre of a cell although not all cells bear tubercles. In section the testa may be about 0·125 to 0·15 mm. thick and shows radial columns with fluted walls, the flutings corresponding with the surface digitations. The testa tends to break along the outlines of these cells. Embryotega with a large rimmed median micropyle. Its cells are square or oblong, much inflated with finely toothed margins. Some of the embryotega cells are as much as 0·05 mm. in diameter. The tegmen is semitranslucent, formed of angular frequently hexagonal thin-walled cells about 0·075 mm. in diameter. The seeds vary greatly in size. Typical measurements are: 1) Length, 1·25 mm.; breadth, 1·25 mm. 2) Length, 1·25 mm.; breadth too crushed to measure. 3) Length, 1·5 mm.; breadth, 1·25 mm. 4) Length, 1 mm.; breadth, 0·8 mm. 5) Length, 1·2 mm.; breadth, 1 mm. 6) Length, 2·6 mm.; breadth, 2·5 mm.

Specimens from the Upper Headon of Colwell Bay range in size from: length, 1·25 to 2·5 mm.; breadth, 1 to 2 mm.

REMARKS. After examining a large number of specimens from the Upper Headon of Colwell Bay, it appears that *Brasenia antiqua* must be regarded as identical with *B. spinosa*, the two types with spiney tubercles and short thick tubercles respectively appear to grade into one another so that they cannot be separated. The variety with thick tubercles was fairly abundant at Hordle, the thin spined variety was scarce. Its small size as well as the large tubercles appear to distinguish this species from the living *B. schreberi* and from all other fossil forms so far seen. *B. spinosa* is known from Bed 10 below Hordle House (V.20041, Chandler, 1925, pl. 3, fig. 5*a*; V.20041*a*, Chandler, 1925, pl. 3, fig. 5*b*; V.43737) and Bed 10 east of Beckton Bunny (V.42121, *a*).

Brasenia oblonga Chandler

(Pl. 25, figs. 44–46)

1925. *Brasenia oblonga* Chandler, p. 23, pl. 3, fig. 6.

DIAGNOSIS. Seed elongate, rounded cylindrical, somewhat truncate at the apex, raphe forming a longitudinal ridge, aperture for embryotega large. Surface tubercled especially at base and along raphe ridge. Also with obscure longitudinal ridges. Length, 1·75 mm.; breadth, 0·9 to 1 mm.

HOLOTYPE. Brit. Mus. (N.H.), No. V.20043.

DESCRIPTION. No additions to this are needed.

REMARKS. Both specimens had lost the embryotega.

Family MENISPERMACEAE

Section COCCULEAE Diels

Subsection COCCULINEAE Diels

Genus ***PALAEOSINOMENIUM*** Chandler, 1961 : 159

Palaeosinomenium obliquatum (Chandler)

(Pl. 25, figs. 47–50)

1925. *Menispermum obliquatum* Chandler, p. 24, pl. 3, fig. 9*a*, *b*.

DIAGNOSIS. Endocarp curved somewhat obliquely, ventral margin slightly concave. Radially aligned ridges conspicuous outside the horse-shoe shaped ridge and on the marginal flange. Foramen between the limbs elongate, its lower end well above a line drawn between the extremities of the two limbs of the endocarp. Diameter about 3 by 4 mm.

HOLOTYPE. Brit. Mus. (N.H.), No. V.20049 (now shattered).

REMARKS. Although the holotype is now much shattered, the characters are also shown by the fresh but imperfect material here illustrated. In the light of fuller experience the species is transferred to the fossil genus *Palaeosinomenium* which is defined as having a more oblique endocarp and a more elongate foramen than the living *Sinomenium* and *Menispermum*. *P. obliquatum* is smaller than *P. venablesi* (Chandler, 1961 : 159, pl. 16, figs. 9–13) and somewhat smaller than *P. pulchrum* (Chandler, 1961 : 329, pl. 33, figs. 5–7) which it very closely resembles but it also has a relatively narrower marginal flange than *P. pulchrum*.

Family LAURACEAE

Genus?

(Pl. 25, figs. 51, 52)

DESCRIPTION. *Berry:* One-carpelled, probably originally subglobose, compressed dorsiventrally in fossilization, seated on a shallow cupule or swollen flattened peduncle, about 3 mm. in diameter, the scar of attachment on the berry about 1·8 mm. in diameter. Epicarp shining, 0·025 to 0·05 mm. thick, with scattered circular depressions, formed of a layer of equiaxial cells which are slightly convex superficially and about 0·016 mm. in diameter. Mesocarp (heavily impregnated with amorphous pyrites as in the London Clay fossils) varying considerably in thickness owing to uneven contraction on drying or crushing, probably averaging originally about 1·5 to 2 mm., its structure obscure. Endocarp 0·15 mm. thick, pointed at the apex, rounded conical, formed of columnar cells in section which are about 0·016 mm. broad. Testa and chalaza not seen but seed probably conforming to the outline of the endocarp the chalaza occupying the base of the rounded conical locule. Transverse diameter of berry (as crushed), 5·6 mm.; height (reduced by compression), 3·5 mm.; diameter of endocarp (not crushed), 3·3 mm.; height of endocarp, 2·6 mm.

REMARKS AND AFFINITIES. Whereas the relationship to Lauraceae is clear, without more and better material no satisfactory generic determination is possible. Clearly the specimen belongs to a small fruited genus with thick endocarp and small cupule (or swollen flattened peduncle). *Cinnamomum*, *Litsea*, and *Lindera* appear to be possible relationships. The circular depressions of the epicarp occur in *Cinnamomum*. C. Reid records leaves of *Cinnamomum* but without figures or descriptions. His specimens are not extant (Reid & Groves, 1921 : 178).

Family DROSERACEAE

Genus *ALDROVANDA* Monti

Aldrovanda ovata (Chandler)

(Pl. 26, figs. 53–55)

1925. *Nuphar ovatum* Chandler, p. 22, pl. 3, fig. 3*a*, *b*.
1926. *Aldrovanda ovata* (Chandler) Reid & Chandler, p. 113, pl. 6, figs. 24–26.

HOLOTYPE. Brit. Mus. (N.H.), No. V.17485.

REMARKS. The discovery of the true relationship of these seeds by Docturowsky following upon work on living *Aldrovanda* by Nikitin and Korzhinsky is reported by Reid & Chandler (1926: 112). Specimens (V.17485–87) from Hordle (precise locality and horizon not specified) were figured by Chandler (1925) and by Reid & Chandler (1926). Also from an unspecified horizon are V.20053*a*,*b*. V.42130 is from Bed 10 east of Beckton Bunny and V.20052 from Bed 31. The same species characterized by its long neck, conspicuous apical mucro, marked raphe ridge and relatively smooth surface, with a thick testa of two coats together measuring nearly a quarter of the diameter of the seed occurs at Colwell Bay in beds presumed to have been Lower Headon (V.42124, V. 42127) and in the *Limnocarpus* Band (V.42128–29). Some seeds both from Hordle and Colwell show the small circular plug closing the narrow neck. It has a central short thick mucro associated with the micropyle from which small convex equiaxial cells diverge over its outer surface increasing in size towards the circumference of the plug. Hilum at the margin of the plug. Dimensions of a number of seeds are as follows : 1) Length of seed, 1·75 mm. ; breadth, 1·35 mm. ; length of neck, 0·25 mm. 2) Length, 1·76 mm. ; breadth, 1·4 mm. ; length of neck, 0·3 mm. 3) Length, 1·9 mm. ; breadth, 1·25 mm. ; length of neck, 0·25 mm. 4) Length, 2 mm. ; breadth, 1·25 mm. ; length of neck, 0·25 mm. 5) Length, 1·75 mm. ; breadth, 1·25 mm. ; length of neck, 0·25 mm. 6) Length, 2 mm. ; breadth, 1·25 mm. ; length of neck, 0·3 mm. The average length of seeds is 1·83 mm. ; average breadth, 1·28 mm. i.e. relatively longer in proportion to the breadth than the specimens from Hordle measured by Reid & Chandler (1926 : 113).

Family HAMAMELIDACEAE

Genus ***EOLIQUIDAMBAR*** nov.

DIAGNOSIS. Agglomerate fruiting head with deep areoles. Carpels splitting into two equal valves which are not produced into awns.

TYPE SPECIES.—*Eoliquidambar hordwellensis* n. sp.

Eoliquidambar hordwellensis n. sp.

(Pl. 26, figs. 56–59)

DIAGNOSIS. That of the genus.

HOLOTYPE. Brit. Mus. (N.H.), No. V.42131*a*.

DESCRIPTION. *Fruiting Head :* Pedunculate, woody agglomerate, ovoid, formed of about eighteen to twenty-five deeply hollowed polygonal areoles each holding a single fruit. Wall between areoles thick, formed of woody fibres radiating from the axis of the fruit. Surface of these walls covered by a shining wrinkled epidermis, the wrinkles parallel with the margins of the areoles. Each wall shows a conspicuous median furrow at the surface, the furrows indicating the plane of fusion between the walls of adjacent areoles. Length of the ripe fruiting head, 17·5 mm. ; transverse diameter, 12·5 mm. Diameter of areoles at surface about 7·5 to 8 mm.

Fruitlets : Capsular, probably two-loculed, splitting at the apex into two valves which are not produced into awns. At the surface of the head the valves are crescentic in outline and are covered by a light coloured shining wrinkled epidermis formed of oblong cells, 0·01 mm. in greatest diameter, aligned parallel with the crescents at the middle of the valves and at right angles to them at the margins. Endocarp and seeds not seen. Length of crescents, 3·5 to 4·5 mm. ; breadth, 1·5 mm.

Remarks. In addition to the holotype there are immature fruiting heads: V.42131 is from Bed 10 between Beckton Bunny and Long Mead End and V.42132 from Bed 10 east of Beckton Bunny. The heads even in the immature condition are easily distinguishable from *Protoaltingia hantonensis* by the single pair of crescentic valves in each areole whereas in *Protoaltingia* even in young heads four knob-like valves are seen. The fibrous agglomerate character and the capsular fruits in the areoles indicate the family Hamamelidaceae section Altingieae. That the absence of awns at the apex of the fruits is an original feature and not due to abrasion is clearly indicated by the well preserved unbroken continuous epidermis covering the external margins of the valves. All living species of *Liquidambar* seen have long persistent styles which form gradually attenuated awns to the valves on dehiscence of the fruit while the margins of the areoles have a complex lobed structure quite unlike the smooth continuous surface of epidermis seen in the fossil. At the same time the mode of dehiscence of the fossil fruitlets into two valves is like that of *Liquidambar*. In this genus dehiscence is septicidal and the endocarps are persistent. The mode of dehiscence is not shown in the fossil and there is no evidence whether or not the endocarps are shed. In *Altingia* and *Protoaltingia* although the styles do not form awns dehiscence is in two planes, septicidal and loculicidal, hence the apex of the fruit is four-partite giving rise to the four knob-like valves mentioned above. It appears, therefore, that the fossil does not agree in all respects with *Altingia, Protoaltingia* or *Liquidambar* and it has been referred to a new genus *Eoliquidambar*.

Genus ***PROTOALTINGIA*** Chandler

Protoaltingia hantonensis Chandler

(Pl. 26, fig. 60)

1925. *Liquidambar* sp. Chandler, p. 25, pl. 4, fig. 1.
Protoaltingia hantonensis Chandler (in press), pl. 9, figs. 18–24; pl. 28, figs. 6–8.

Description. *Fruiting head:* Always so much abraded that the complete head is not preserved so far as is known at Hordle, but the specimen (V.20054) originally figured appears to have been ovoid although the long axis was erroneously oriented transversely. Agglomerate, with numerous funnel-like alveolae showing fibrous but somewhat cavernous walls the bases only remaining. These alveolae hold the worn down persistent fruitlets, one in each alveole. Largest fragment now preserved about 5 to 7 mm. in diameter.

Fruitlets: Capsular, two-loculed with antero-posterior locules formed of transverse fibres, elongate as seen in transverse section at right angles to the septum. Septicidal as shown by the curvature and separation of the walls at the septum. Evidence of loculicidal dehiscence almost destroyed by the wearing away of the distal ends of the fruit walls but indicated in one or two alveolae by the thinning and curvature of the walls in the plane at right angles to the septum.

Remarks. With the help of well-preserved material from the Bournemouth Beds these fragmentary remains can be better understood than in 1925 when they were erroneously referred to *Liquidambar* itself through lack of understanding of the characters of the fossil combined with lack of knowledge of the living genus. The reference to Hamamelidaceae was correct. The account of the Bournemouth fruits is in the press. The Hordle specimens despite their poor condition agree with them in the characters seen. The elongate form of the fruitlets at right angles to the septum in transverse section allies them with *Protoaltingia hantonensis* and not with *Eoliquidambar hordwellensis* (p. 120). In addition to the figured fruit (now more broken) and V.20056 from the contemporary channel west of Long Mead End, there are also a few fragmentary heads from Bed 10, east of Beckton Bunny (V.20055, V.42133).

Family ROSACEAE

Genus ***RUBUS*** (Tourn.) L.

Rubus acutiformis Chandler

1925. *Rubus acutiformis* Chandler, p. 26, pl. 4, fig. 2.
Rubus acutiformis Chandler : Chandler (in press), pl. 4, figs. 36–40.

There is nothing to add to the descriptions already published except that the endocarps occur in the greatest abundance in Bed 10 at the cliff base below Hordle House (V.20057–58, V.42134) and more rarely east of Beckton Bunny (V.42135). Specimens from Studland (in press), Bournemouth Freshwater Beds and Cliff End (awaiting publication) appear to be identical but the Hordle specimens are much better preserved than those from other localities.

Family LEGUMINOSAE?

Genus?

(Pl. 26, fig. 61)

DESCRIPTION. *Seed :* Smooth broadly subovoid or subglobular having a very slight and inconspicuous bisymmetry, probably splitting down one side in the plane of symmetry where a finished suture can be seen. Hilum marked by an obscure projection on the margin. Surface of fine equiaxial cells, 0·01 mm. in diameter, the testa compact 0·2 to 0·4 mm. thick, becoming thinner towards the hilum, columnar in section the fine columns, about 0·01 mm. broad and apparently formed of short cells placed accurately end to end. Length of seed, 4·5 mm. ; breadth, 4 mm. ; thickness rather less than breadth but as the seed has burst it cannot be measured accurately. The seed shows no outstanding readily recognizable characters, but the general appearance and testa structure suggest Leguminosae.

Genus?

(Pl. 26, fig. 62)

DESCRIPTION. *Seed :* Oval in outline, much compressed, compression increased in fossilization so that the opposite walls are now in contact, having a small marginal circular hilum, 0·25 mm. in diameter, situated near the end of one of the long margins. This hilar scar is surrounded by a somewhat rough tumescent area on both surfaces. Elsewhere the surface of the seed is smooth and shining, one side showing an obscure curved groove sub-parallel with the circumference, its extremities arising at the hilar region. Testa superficially pitted, pits 0·004 to 0·005 mm. in diameter, somewhat obscured over much of the surface by tension fissures and striae. Thickness of testa 0·15 to 0·25 mm., formed of radially aligned cells having an obscure columnar appearance. Inner surface of convex equiaxial cells 0·1 mm. in diameter. Length of seed, 5·5 mm. ; breadth, 3·75 mm. ; thickness, 1 mm.

REMARKS AND AFFINITIES. One seed broken obliquely into two fragments, with a third small fragment missing on the dorsal margin. The form of the seed and character of the hilum suggest possible relationship with Leguminosae, but the nearer affinities have not been found. There is no distinct inner coat inside the columnar coat as in *Acacia* or *Albizzia* nor is the testa conspicuously columnar as in these and many other Leguminosae seeds.

Family RUTACEAE

Genus ***ZANTHOXYLUM*** Linnaeus

Zanthoxylum hordwellense n. sp.

(Pl. 26, figs. 63, 64)

1925. *Zanthoxylon* cf. *ailanthoides* Sieb. & Zucc. : Chandler, p. 26, pl. 4, fig. 3*a*, *b* ; text-fig. 9.

DIAGNOSIS. Seed with very slightly convex ventral margin, sides less inflated than living *Z. ailanthoides*. Surface with concentric wrinkles but few or no connecting ridges. Orifice to raphe canal ventral not basiventral. Length of seed, 2·25 to 4·5 mm. ; breadth, 2·25 to 3·5 mm. ; thickness, 1·85 to 2·75 mm.

HOLOTYPE. Brit. Mus. (N.H.), No. V.20059.

DESCRIPTION. *Seed :* Semi-anatropous, gibbous in outline having the ventral margin slightly convex, the dorsal rounded. Somewhat laterally flattened especially on each side of the ventral margin which is occupied by an elongate-triangular depressed hilar scar. Chalaza basal on the ventral side of the longest axis of the seed, marked by a large circular internal aperture (V.20059*a*) ; raphe canal prominent with a conspicuous orifice at the lower end of the hilar scar (Pl. 26, fig. 64) ; micropyle terminal on the ventral margin at the opposite end of the scar to the raphe orifice ; epidermis thin, shining, black, ornamented with a few concentric wrinkles and fine polygonal equiaxial pits ; within is a thick coat formed of equiaxial cells. Dimensions of seeds : 1) Length, 3·5 mm. ; breadth, 3 mm. ; thickness, 2·75 mm. 2) Length, 4 mm. ; breadth, 3 mm. ; thickness, 1·85 mm. ; length of hilar scar, 3 mm. 3) Length, 3·25 mm. ; breadth, 2·5 mm. ; thickness, 2·25 mm. ; length of hilar scar, 2·5 mm. 4) Length, 4·5 mm. ; breadth, 3·5 mm. ; thickness, 2·25 mm. Other small seeds varied in length or breadth from 2·25 to 2·75 mm. A typical scar measured 0·65 by 0·19 mm.

REMARKS AND AFFINITIES. Seeds fairly abundant, although very liable to decay, occurring in Bed 10 below Hordle House (V.20059–60) and east of Beckton Bunny (V.42136). Usually the thin black epidermis has been destroyed and the thick inner integument is heavily impregnated with pyrites. It was pointed out (Chandler, 1925 : 27) that there is a close resemblance to *Zanthoxylum* (*Fagara*) *ailanthoides* Sieb. & Zucc. from which the fossil differs in the rarity or absence of transverse ridges connecting the concentric wrinkles, in its lesser degree of inflation, in its less convex ventral margin and its ventral orifice to the raphe canal as contrasted with the basiventral orifice of the living. Additional fossils since found merely increase the known variation in size of the species which further experience suggests deserves a distinct name. It is therefore called *Z. hordwellense*.

Zanthoxylum compressum Chandler

(Pl. 26, figs. 65–67 ; Text-fig. 3)

1925. *Zanthoxylon compressum* Chandler, p. 28, pl. 4, fig. 5.

Diagnosis. Seed rounded subquadrangular in outline, broadest dorsiventrally. Hilum very short, concave. Length of seed parallel with hilar scar, 3·25 to 3·5 mm. ; maximum diameter, 3·75 to 4 mm. approximately at right angles to scar.

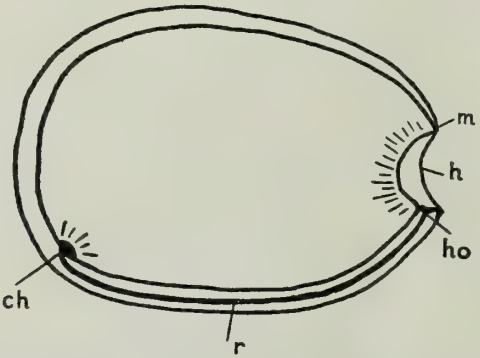

Fig. 3. *Zanthoxylum compressum* Chandler. Longitudinal section through a seed to show relative positions of hilar scar (*h*), hilar opening (*ho*), raphe (*r*) and chalaza (*ch*). × 12 approx.

Holotype. Brit. Mus. (N.H.), No. V.20061.

Description. (Slightly emended) *Seed :* Semi-anatropous, rounded subquadrangular in outline, broadest dorsiventrally, much compressed. Ventral margin short, concave, occupied by the sunk subtriangular hilar scar. Opposite margin rounded, the internal chalaza being situated where this rounded margin gradually merges into the lower long lateral margin of the seed (as revealed by a break in the testa of the second specimen). Raphe, connecting the lower broad end of the hilar scar with the chalaza, a long canal which traverses the testa within the long lower lateral margin of the seed. Outer surface black and shining ornamented with finely crenulate pits like those on the middle black coat of some living species. A second seed (V.42137) was abraded and rough superficially but retained a tiny fragment of a black shining superficial layer with slightly convex, equiaxial angular cells about 0·05 mm. in diameter. These cells are separated by fine hair-like straight raised walls. Tegmen thin, of equiaxial cells 0·016 to 0·025 mm. in diameter. Length of holotype (parallel with hilar scar), 3·5 mm.; breadth (maximum diameter), 4 mm. Length of second abraded seed, 3·25 mm.; breadth (maximum diameter), 3·75 mm.; thickness, 1·5 mm. In this specimen the hilar scar was considerably shorter than in the first seed. Thickness of wall where broken at chalaza, 0·3 mm.

REMARKS. Two seeds clearly related to *Zanthoxylum* distinguished specifically by the broad subquadrangular rounded form and very short hilum.

Genus ***PHELLODENDRON*** Rupr.

Phellodendron costatum Chandler

1925. *Phellodendron costatum* Chandler, p. 28, pl. 4, fig. 6*a–c*.
Phellodendron costatum Chandler: Chandler (in press), pl. 10, fig. 1.

DIAGNOSIS. Seed sometimes with knob-like subapical constriction. More inflated than any living species. Longitudinal ribs unusually well marked. Length, 3 to 3·5 mm., breadth, 1·8 to 2·25 mm.; thickness 1·8 to 2 mm.

HOLOTYPE. Brit. Mus. (N.H.), No. V.20062.

EMENDED DESCRIPTION. *Seed:* Semi-anatropous, subovoid, bisymmetric, with a more or less straight ventral margin and a rounded dorsal margin in the plane of symmetry; apex curved slightly towards the ventral side, sometimes with a knob due to an inconspicuous subapical constriction. Hilum strap-shaped, extending almost the whole length of the ventral margin, micropyle sunk in a depression at the apical end of the hilar scar i.e. on the knob when present; raphe canal opening at a foramen at the base of the hilar scar, short, curved; chalaza a large circular internal aperture at the end of the major axis of the seed away from the micropyle. Germination by splitting in the plane of symmetry; surface sculpture of numerous acute longitudinal ribs (about twenty-four were counted in one specimen) frequently connected by transverse spurs; finer structure of small cells equiaxial or transversely elongate at right angles to the ribs. Testa in section 0·3 mm. thick at the middle of the broad surface, formed of square cells about 0·02 to 0·025 mm. in diameter arranged in radial rows. Length of seed, 3 to 3·5 mm.; breadth, 1·8 to 2·25 mm.; thickness, 1·8 to 2 mm.

REMARKS AND AFFINITIES. In addition to the holotype there are four other seeds (V.42138–41). The species is now also known from the Dorset Pipe-clay Series at Arne (in press) and the Bournemouth Freshwater Beds at Sandbanks (awaiting publication). The form, character of hilum, raphe and chalaza and testa structure all relate these specimens to Rutaceae. Although the form and ornamentation in general and the strap-shaped hilar scar indicate *Phellodendron* as the nearest living genus, the fossil seeds are clearly distinguished from any living or other fossil species by the greater degree of inflation, somewhat smaller size and more marked longitudinal ribs of the surface. On account of this last feature the name *P. costatum* was given.

Genus ***RUTASPERMUM*** Chandler, 1957 : 102

Rutaspermum ornatum (Chandler)

(Pl. 26, fig. 68 ; pl. 27, figs. 69–71)

1925. *Zanthoxylon ornatum* Chandler, p. 27, pl. 4, fig. 4*a*, *b* ; text-fig. 10.

Diagnosis. Seed broadly semilunate in outline with straight ventral margin slightly beaked at the micropyle, hilar depression up to three-quarters of the length of the seed. External surface ornamented with sinuous longitudinal ribs which occasionally branch and anastomoze, sometimes connected by short transverse ribs. Testa conspicuously pitted, smooth around the hilar depression. Length of seeds, 4 to 7·25 mm. ; breadth, 3·5 to 4 mm. ; thickness, 2·5 to 3 mm.

Neotype. Brit. Mus. (N.H.), No. V.42142. (Holotype decayed.)

Description. *Seed :* Semi-anatropous, broadly semilunate in outline, inflated. Ventral margin more or less straight, slightly beaked above, occupied in the upper part by the elongate narrowly triangular hilar depression which extends from the apex for nearly three-quarters of the length in some specimens, two-thirds of the length in others and usually well below the middle. Chalaza marked internally by a large orifice situated at the extremity of the longest axis remote from the apical beak. External surface ornamented with sinuous longitudinal ribs which occasionally branch and anastomoze or are sometimes connected by short transverse ribs. Surface formed of equiaxial or elongate pits, 0·025 to 0·03 mm. in diameter. Testa about 0·3 to 0·4 mm. thick on the dorsal side, thicker on the ventral side. Completely surrounding the hilar depression is a smooth somewhat flattened area. A few seeds show traces of a thin black shining pitted epidermis but this is almost invariably destroyed. Length of seeds, 4 to 7·25 mm. (frequently about 4·5 mm.) ; breadth, 3·5 to 4 mm. ; thickness, 2·5 to 3 mm. Typical measurements are : 1) Length, 5·5 mm. ; breadth, 4 mm. ; thickness, 2·5 mm. 2) Length, 4·5 mm. ; breadth, 3·5 mm. ; thickness, 2·5 mm. 3) Length, 5·5 mm. ; breadth, 4 mm. ; thickness, 3 mm. 4) Length, 6 mm. ; breadth, 4·5 mm. ; thickness, 3 mm. 5) Length, 5 mm. ; breadth, 3·5 mm. ; thickness, 3 mm.

Remarks and affinities. Numerous seeds (cf. V.42146) almost invariably preserved in a soft pyrites mud which is peculiarly liable to rapid decay on exposure to air. At first these seeds were referred to the genus *Zanthoxylum* but it is now clear that no living representative of *Zanthoxylum* has such clearly defined regular superficial ornamentation, hence they are now relegated to the form-genus *Rutaspermum* Chandler, no comparable living genus having been found. The species is distinguished clearly from all others from the south coast deposits by the combined characters of size and smooth unornamented area immediately surrounding the hilar scar.

Family Burseraceae

Genus ***PALAEOBURSERA*** Chandler, 1961 : 202

Palaeobursera lakensis Chandler

(Pl. 27, figs. 74, 75)

Palaeobursera lakensis Chandler (in press), pl. 10, figs. 20–26.

Description. *Pyrene :* Pointed-ovate in outline, subtriangular in transverse section, dorsal surface convex, ovate ; ventrilateral surfaces meeting to form a median ventral longitudinal angle especially clear in the upper two-thirds. Angle pierced about 2 mm. from the apex (i.e. below the middle) by a curved transverse aperture, concave towards the apex of the fruit, for the ingress of the funicle to the placenta. Germination valve occupying the upper two-thirds of the dorsal surface. Wall formed superficially of equiaxial pits about 0·03 to 0·05 mm. in diameter over most of the surface but becoming narrower and elongate along the ventral angle where they may be 0·016 mm. broad and 0·03 to 0·05 mm. long. Thickness of wall on dorsal side 0·1 mm. Small cells, about 0·01 mm. in diameter can be seen forming the walls of the large external pits. Length of endocarp, 3·5 mm. ; breadth, 2·75 mm. ; thickness, 1 mm.

Remarks and affinities. A perfect specimen (V.42147) and three other fragments (V.42148), one the rounded end of a larger pyrene. A comparison with pyrenes from the Dorset Pipe-clay Series of Lake (in press) and the Bournemouth Freshwater Beds at Sandbanks (awaiting publication) indicates that the Hordle specimens belong to the same species. It must be noted that the best preserved Lower Headon pyrene is a broad example, uncrushed (as is often the case in the Hordle fossils) and therefore more inflated. Its surface is well preserved unlike the older specimens which are both abraded and sand pitted, but identical pits have been seen in a pyrene from Sandbanks and in other fragments. The Hordle pyrene is therefore referred to *P. lakensis* Chandler.

Family Anacardiaceae

Section Spondieae

Genus?

(Pl. 27, figs. 72, 73)

Description. Part of a thin-walled fruit with obscure cell structure and rough external surface. Two compartments are occupied by bolster-shaped closely adpressed bodies which may be resin sacs as in *Dracontocarya glandulosa* from the Dorset Pipe-clay Series (Chandler (in press), pl. 12, figs. 10–21). These bodies appear to have been partially released by maceration so that they resemble lines of parietal seeds. The exposed surface is ornamented by a network of fine ridges forming irregular polygonal areas about 0·025 to 0·05 mm. in diameter. The fruit fragment is 2·5 by 3 by 1·5 mm. The sacs vary, those measured were respectively: 0·4 by 0·25 mm.; 1·2 by 0·6 mm. at one end and 0·3 mm. at the other end; 0·6 by 0·2 mm.; 1 by 0·3 mm.

REMARKS. No true locules or seeds have been seen nor is the form of the perfect fruit known. While the presence of the resin sacs suggests relationship with Spondieae, the fragment cannot be identified with *Dracontocarya glandulosa* to which it bears a general resemblance as the endocarp in that species is much more fibrous and its sacs are larger (about 0·912 to 1·9 mm. long).

Family ICACINACEAE

Genus ***NATSIATUM*** Buch.-Ham.

Natsiatum eocenicum Chandler

1925. *Natsiatum eocenicum* Chandler, p. 29, pl. 4, fig. *7a–d*; text-fig. 11.
Natsiatum eocenicum Chandler: Chandler (in press), pl. 13, figs. 6–16.

The endocarps have been redescribed (see above) in an account of the species from the Dorset Pipe-clay Series and some fresh Hordle material illustrated for comparison. V.40614 (the neotype), V.42151–52 (fragments) are from Bed 10 east of Beckton Bunny. V.40615–16 from Bed 10 below Hordle House. The original holotype, V.42149, (Chandler, 1925, pl. 4, fig. *7b–d*) is now much broken and decayed as is V.42150 (Chandler, 1925, pl. 4, fig. *7a*). Both were from the contemporary stream channel west of Long Mead End.

? *Iodes* sp. (or **? *Natsiatum*** sp.)

(Pl. 27, figs. 76, 77)

1925. *Iodes* sp., Chandler, p. 29, pl. 4, fig. 10; text-fig. 12.

DESCRIPTION. *Endocarp*: Incomplete, only the funicular margin being preserved. Longitudinal section narrow-ovate, the lateral funicular canal gradually broadening at the apex; placenta subapical on the funicular margin marked externally by a pair of short horn-like processes which flank it. Walls thick and woody. External surface ornamented by a few conspicuous ridges which branch and anastomoze to form a very coarse network. Locule lining thin, semitranslucent, formed of inflated equiaxial cells. Length of fragment, 9·75 mm.; incomplete breadth, 4 mm.; thickness, 5·75 mm.

REMARKS. V.20063, Bed 10 below Hordle House. Relationship to Icacinaceae indicated by the character of the funicular margin. The form of the longitudinal section recalls *Natsiatum herpeticum* Ham. and species of *Iodes*. The convex cells of the locule lining recall *Natsiatum* rather than *Iodes* but the relationship must remain uncertain without better material.

Genus *IODES* Blume

Iodes ? hordwellensis n. sp.

(Pl. 27, figs. 78, 79 ; Text-fig. 4)

Diagnosis. Endocarp broader than long, much inflated. Ridges of surface ornamentation somewhat rounded, not acute like those of *Natsiatum eocenicum*. Length, 6·5 mm. ; breadth, 8·5 mm. ; thickness about 5 mm.

Holotype. Brit. Mus. (N.H.), No. V.42153.

Description. *Endocarp :* Similar superficially to that of *Natsiatum eocenicum* but broader than long and much more inflated. Bisymmetric about a plane passing through funicle, attachment and style. Funicular margin having a rounded rib which broadens conspicuously over the subapical placenta. Opposite margin with a sharper ridge. Style apical, marked by a small knob. External surface with a network of rounded ridges less prominent and acute than in *N. eocenicum*, surface formed of fine equiaxial cells, finer than those of *N. eocenicum*. A small fragment (V.42154) of a second specimen? shows a similar curvature. On its inner surface there are obscure digitate cells covered by a thin integument bearing small papillae. Length of endocarp (possibly slightly reduced by distortion), 6·5 mm. ; breadth, 8·5 mm. ; thickness (possibly slightly increased by distortion), 5 mm.

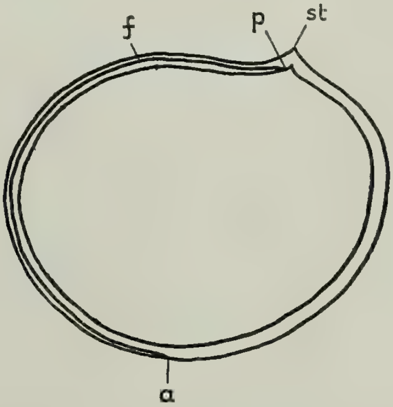

Fig. 4. *Iodes ? hordwellensis* n. sp. Diagram to show endocarp in longitudinal section. (*st*) style, (*p*) placenta, (*f*) funicle, (*a*) attachment. ×4 approx.

Remarks and affinities. One endocarp and a fragment. The species is clearly distinguished by its broad transverse form and less sharp ridges from *Natsiatum eocenicum*. The appearance and papillae of the locule lining of the second specimen suggest relationship with *Iodes*, but the transversely broad form has not been seen in this genus. Hence the determination is regarded as provisional.

Genus *ICACINICARYA* Reid & Chandler, 1933 : 344

Icacinicarya transversalis n. sp.

(Pl. 27, figs. 80–82)

DIAGNOSIS. Endocarp transversely-oval in outline. Style asymmetric on the broad apical margin, attachment near middle of broad basal margin. External surface with network of bold sharp ridges. Locule tubercled. Length of uncrushed valve, 10·25 mm. ; breadth, 14 mm.

HOLOTYPE. Brit. Mus. (N.H.), No. V.23420.

DESCRIPTION. *Endocarp :* Woody, transversely-oval in outline, somewhat compressed, bisymmetric about a plane which includes the two major axes and the funicle and style, dehiscing in this plane into symmetrical halves. Attachment near the middle of the broad basal margin, style asymmetric on the broad apical margin, so that a straight line drawn between these two organs divides the endocarp unequally. Funicle marginal within the thickness of the wall in the larger of the two unequal divisions described, placenta apical adjacent to the stylar canal, marked externally by a slight thickening of the margin ; seed pendulous, solitary. Endocarp from 0·3 to 0·35 mm. thick, hard and compact, formed of cells, 0·016 mm. in diameter arranged in a somewhat columnar manner as seen in sections of the wall, the " columns " in parts being somewhat oblique. External surface boldly ornamented by a network of sharp ridges, some of these given off from the margin with the funicle are longer, straighter and more conspicuous than the others. Locule tubercled, the tubercles formed by a coat of convex cells. Length of specimen, 10·25 mm. ; breadth, 14 mm. Length of a distorted endocarp, probably referable to the same species, imperfect ; breadth, 10 mm.

Seed : Represented by shrivelled and half-decayed testa, formed of equiaxial cells, somewhat irregular in shape and alignment, about 0·025 mm. in diameter.

REMARKS AND AFFINITIES. A valve (V.23420) from Bed 10 below Hordle House having a small fragment missing on the funicular margin. Also a much distorted endocarp (V.23419). It was imperfect at the apex, with better preserved ornamentation than that of V.23420 but probably belonged to the same species. This imperfect specimen was dissected after it had been photographed ; it then showed the remains of the seed and the tubercles of the locule lining.

Form and structure indicate relationship with Icacinaceae. The broad oval form also seen in the smaller endocarps of *Iodes? hordwellensis* has not so far been found among living representatives of the family but occurs in fossil forms from the London Clay e.g. *Faboidea crassicutis* (Reid & Chandler, 1933 : 341, pl. 16, figs. 3–10) and *Icacinicarya reticulata* (Chandler, 1961 : 225, pl. 22, figs. 25–34).

Icacinicarya becktonensis n. sp.

(Pl. 27, figs. 83, 84)

DIAGNOSIS. Endocarp bisymmetric, subobovoid, funicular margin only slightly convex, opposite margin almost semicircular in plane of symmetry. Funicular canal broad. Surface coarsely but very obscurely reticulate. Length of endocarp (slightly imperfect at style), 4 mm. ; breadth in plane of symmetry, 3 mm. ; thickness at right angles to plane of symmetry, 2·5 mm.

HOLOTYPE. Brit. Mus. (N.H.), No. V.42155.

DESCRIPTION. *Endocarp :* subobovoid, bisymmetric, lateral funicle in plane of symmetry broad, incurving abruptly at the apex to the placenta. Margin carrying funicle only slightly convex, opposite margin almost semicircular in plane of symmetry. No evidence is preserved of short projecting horns or canals flanking the style at the apex, probably because the apex and outer walls of the funicular canal are abraded. Surface showing a few coarse rather obscure reticulations. Small coarsely digitate cells can be seen in patches. Wall (as preserved) 0·228 mm. thick.

Seed : Represented only by a few patches of testa or by impressions on a film of pyrites, formed of equiaxial angular cells about 0·013 mm. in diameter. A large circular scar with rimmed edge originally lay within the broken apex of the endocarp and clearly represented the hilum of the seed. Dimensions of seed somewhat smaller than those of the endocarp, too incomplete to measure.

REMARKS. The specimen was originally perfect apart from its abraded condition which exposed the funicular canal. It subsequently collapsed showing the wall in section almost entirely replaced by amorphous pyrites except for a film of carbonaceous substance lining it outside and in. The species resembles *Icacinicarya pygmaea* (Chandler, 1960 : 226, pl. 34, figs. 118–121) in its somewhat gibbous outline with slightly convex funicular margin and highly convex opposite margin, but is more obovoid in shape than that species and considerably larger. There is no evidence of short apical canals flanking the style as in *I. pygmaea.* It is also distinguished from the subglobular endocarps of *I. bartonensis* (Chandler, 1960 : 227, pl. 34, fig. 122) by its larger size and subobovoid form.

Family RHAMNACEAE

Genus ***RHAMNUS*** Linnaeus

Sub-genus ***FRANGULA*** Tourn. ex Hall.

Frangula hordwellensis n. sp.

(Pl. 27, figs. 85, 86 ; pl. 28, fig. 87)

1925. Rhamnaceae ? Genus ? sp. 2, Chandler, p. 31.
1926. Rhamnaceae Genus ? sp. 2, Chandler, pl. 5, fig. 2.

DIAGNOSIS. Pyrene and seed together 3·5 to 5·25 mm. long ; 3·6 to 3·75 mm. broad. Oboval or suboboval in outline with emarginate distal end.

HOLOTYPE. Brit. Mus. (N.H), No. V.42156.

DESCRIPTION. *Fruit :* A globose berry 6·25 mm. long, 4 mm. broad in the one specimen found with obscure structure having two pyrenes (or cocci) preserved. Each pyrene formed of a single seed closely embraced by the endocarp except at the extreme proximal end where it projects beyond the carpellary coat; outline of pyrene oboval or suboboval but slightly asymmetric because one margin is a little longer than the other, conspicuously emarginate at the distal end, gently convex with a narrow median longitudinal concavity on one surface and an obtuse but clearly defined median longitudinal angle on the other; formed superficially of concave equiaxial cells, 0·016 to 0·025 mm. in diameter, beneath which are several layers of fibres that diverge obliquely upward from the median angle on the one face, and sweep transversely across the gently convex face. Dimensions of two pyrenes from different fruits: 1) Length, 3·5 mm.; breadth, 3·75 mm. 2) Length, 5·25 mm.; breadth, 3·6 mm.

Seed: Anatropous with marginal raphe; agreeing in shape with the closely investing endocarp but projecting at its proximal end as described. Hilar end with a deep elongate-oval hollow surrounded by a rim formed by an upstanding arillus or projection of the testa. Within the hollow is a median ridge parallel with the broad face of the seed. The raphe enters the testa at one end of the hollow and can be traced along the shorter lateral margin of the seed; the micropyle is at the opposite end of the hollow. Testa black and shining, 0·2 mm. thick around the basal hollow, only about 0·1 mm. thick at the middle of the lateral margin, formed superficially of digitate cells, about 0·025 mm. in diameter, markedly columnar in section, the columns about 0·025 mm. broad, having uneven sinuous walls owing to the variation in diameter of the short cells, arranged end to end, of which they are formed. Seed cavity with a shallow median longitudinal furrowed angle (underlying the external furrow of the pyrene) from which the cells of the internal surface appear to diverge. Tegmen thin, semitranslucent, readily detachable, formed of elongate cells which produce parallel striae about 0·008 mm. apart near the lateral margins, elsewhere of equiaxial cells, 0·012 to 0·016 mm. in diameter. Chalaza a conspicuous thickened scar with branching fibres at the end of the tegmen which immediately underlies the emargination of the seed. Dimensions of seeds approximately those of the pyrenes.

REMARKS AND AFFINITIES. One fruit in a much decayed condition with two seeds preserved was originally described but is now completely decayed. One larger perfect detached seed and part of another (V.42157) have since been found which have added considerably to the knowledge of the structure recorded in 1925.

The endocarp is preserved only in patches on these seeds, the distintegrating processes of fossilization having separated testa and endocarp in a way difficult to effect in living material without maceration.

It is now clear that the relationship is with the sub-genus *Frangula* of the genus *Rhamnus*. Comparison has been made with *R. frangula* Linn. and *R. purshiana* DC. The more slender form and emarginate apex distinguish the fossil from either of these living species, but the general resemblance especially to *R. purshiana* is very close. *R. purshiana* is a native of the Rocky Mountains. The sub-genus *Frangula* is largely American occurring in both the east and west of North America and in South America also. Species are found in Europe, Central Asia, North Africa, the Canaries and the Azores, the mountains of South Europe, the Caucasus and Persia and in Japan.

Family SABIACEAE

Genus *MELIOSMA* Blume

Meliosma sp.

(Pl. 28, figs. 88, 89)

DESCRIPTION. *Endocarp :* One loculed, one seeded, ovoid, bisymmetric in a plane through the attachment and major axis, each broad face with a median broad rounded ridge which extends from the apex to about the middle. Attachment marked by a conspicuous circular aperture. Character of funicular canal not seen. Surface of endocarp showing equiaxial pits about 0·016 mm. in diameter ; thickness of wall about 0·15 mm. of similar cells no definite alignment detected. Lining of endocarp of elongate cells with finely digitate walls their length rather obscure, breadth about 0·01 mm. Testa thin, semitranslucent, formed of inflated longitudinally elongate cells about 0·01 mm. broad, length obscure. Maximum diameter in plane of symmetry, 2·75 mm. ; diameter at right angles to this in plane of symmetry, 2 mm. ; diameter at right angles to plane of symmetry, 1·25 mm.

REMARKS. Two endocarps now shattered but represented by remains with cell structure. They closely resemble material awaiting publication from the Bournemouth Beds and are similar in their small size. The highly characteristic digitate cells lining the locule confirm the ascription based on form and structure to the genus *Meliosma*.

Family VITACEAE

Genus *PARTHENOCISSUS* Planchon

Parthenocissus hordwellensis n. sp.

(Pl. 28, figs. 90–95)

1926. *Parthenocissus* sp., Chandler, p. 33, pl. 6, fig. 1*a–c*.

DIAGNOSIS. Apex of seed flattened or scarcely furrowed, raphe somewhat sunk above the chalaza ; chalaza oval, median, sunk. Ventral infolds more than three-quarters of the length of the seed, diverging upwards. Length of ripe seeds, 3·5 to 5 mm. ; breadth, 2 to 3·5 mm. ; thickness about 2 mm.

HOLOTYPE. Brit. Mus. (N.H.), No. V.20066.

DESCRIPTION. *Seed :* Obovate in outline, smooth, narrowed gradually to the stipitate base, apex slightly flattened or scarcely furrowed. Dorsal surface convex with a median oval slightly sunk chalaza passing abruptly into the narrow somewhat sunk raphe. Ventral angle about 90° when uncrushed, deep lateral depressions extend almost from the base for more than three-quarters of the length and diverge upwards. Surface pitted, pits separated from adjacent ones by their own diameter. Length of seed, 3·5 to 5 mm. ; breadth, 2 to 3·5 mm. ; thickness (uncrushed), 1·5 to 2 mm. A typical seed measured 4 by 2 by 2 mm. Smaller seeds about 2·75 by 1·6 by 1·5 mm. appear to be immature.

Remarks and affinities. The seeds being brittle are often broken. Several specimens (V.42161–64) including an immature seed have been found and a few fragments (V.20067). The species is closely comparable with the living *P. henryi* Hems.

A single seed of *P. hordwellensis* (V.42237) was found in the Barton Beds, Horizon A3, after the paper dealing with Barton plants was in proof. It is an internal cast in pyrites, 4·5 mm. long, 2·5 mm. broad. The ventral surface shows the infolds clearly but the chalaza on the dorsal side is obscured by a coarse crystalline efflorescence. The seed is shown for comparison with the Hordle material in Pl. 28, figs. 94, 95.

Genus ***AMPELOPSIS*** (L. C. Rich. in) Michx.

Ampelopsis rotundata Chandler

1926. *Ampelopsis rotundata* Chandler, p. 33, pl. 5, fig. 5*a–c*.

Diagnosis. Seed roundly obovate in outline, much inflated, apex rounded, base acutely pointed. Dorsal face rounded with raised convex oval chalaza and prominent raphe. Ventral face convex with short divergent deep wide infolds. Length of largest seed, 3·5 mm.; breadth, 3 mm. Length of smallest, 2·5 mm.; breadth, 2 mm.

Holotype. Brit. Mus. (N.H.), No. V.20068.

Remarks. Other material (V.20068*a*) a small immature seed and three incomplete specimens. All the seeds are from Bed 10 near Long Mead End.

Genus ***TETRASTIGMA*** Planchon

Tetrastigma lobata Chandler

(Pl. 28, figs. 96, 97)

1925. *Tetrastigma lobata* Chandler, p. 32.
1926. *Tetrastigma lobata* Chandler, pl. 5, fig. 3*a–c*.
? *Tetrastigma lobata* Chandler; Chandler (in press), pl. 15, figs. 35–38.

Diagnosis. Seed deeply grooved at apex, base tapering or broad and slightly stipitate. Median chalaza oval sunk, raphe narrow sunk. Both surfaces lobed, lobes of ventral surface on both sides and on raphe ridge. Length of seed, 5·5 to 9 mm.; breadth, 4 to 10 mm. in well developed seeds.

Holotype. Completely decayed as is all other material. See Chandler, 1926, pl. 5, fig. 3*b*, *c*.

Description. *Seed:* Obovate, roundly oblong or subcircular in outline, much compressed dorsiventrally, apex deeply grooved, base tapering or broad and slightly stipitate; dorsal face with small sunk median oval chalaza and narrow sunk raphe; surface deeply lobed, lobes radiating from the chalaza. Ventral face with longitudinal infolds from which rounded lobes diverge both over the sides and the raphe ridge. Surface pitted, testa columnar in section. Length of seed, 5·5 to 6·5 or even 9 mm.; breadth, 4 to 10 mm. An exceptionally small seed was 3 mm. long, 3·25 mm. broad. A typical seed was 6·5 mm. long, 5 mm. broad, 3 mm. thick, but the measurements were made after drying so that the seed had contracted to perhaps two-thirds of its original size.

REMARKS. Three seeds of which two were figured in 1926 and one in the present volume. The mode of preservation was such that the species was peculiarly liable to decay. The relationship to living *Tetrastigma* was discussed by Chandler (1925 : 32) and a similar seed referred to *? T. lobata* was described from the Dorset Pipe-clay Series of Lake (in press). Kirchheimer describes a comparable species of *Tetrastigma* under the name *T. chandleri* from the Middle to Upper Oligocene of Saxony (Kirchheimer, 1957 : 324, 602, fig. 197*a–d*) which he states is relatively narrower in proportion to the length.

Family DILLENIACEAE

Genus ***ACTINIDIA*** Lindl.

Actinidia sp.

(Pl. 28, fig. 98)

DESCRIPTION. *Seed:* A fragment showing the rounded apex but unfortunately neither the raphe, micropyle or hilum are preserved. The testa has coarse hexagonal external pits, 0·05 to 0·1 mm. in diameter, delimited by rounded walls with median suture line along which it tends to break. Internally there are corresponding convexities characteristic of *Actinidia*. The fragment is 1·5 mm. long and its maximum breadth is 1 mm.

REMARKS. The seed in spite of its imperfect condition appears to be identical with better preserved material from Bournemouth awaiting publication in which all the distinctive characteristics of *Actinidia* are shown.

Family THEACEAE

Section THEAE

Genus ***GORDONIA*** Ellis

Gordonia minima Chandler

(Pl. 28, figs. 99–102)

1926. *Gordonia minima* Chandler, p. 34, pl. 6, fig. 3*a*, *b*; text-fig. 16.

DIAGNOSIS. Capsule pointed-ovoid, scar of attachment small so as scarcely to truncate the base. Sutures of five valves forming thin longitudinal ridges. Length of capsule, 8·5 to 10 mm.; breadth, 4 to 5·75 mm.

HOLOTYPE. Brit. Mus. (N.H.), No. V.20070.

DESCRIPTION. *Fruit:* A five-loculed woody capsule with five loculicidal thick-walled valves which remain attached to one another and to the receptacle at the base; capsule pointed-ovoid the apex much attenuated, scar of attachment small, remains of receptacle persistent, prominent, circular or pentagonal. The sutures of the valves form thin longitudinal external ridges. Valves triangular in cross section, before dehiscence united throughout their length by thin septa to a five-angled columella. On dehiscence the septa break away at the base along a curved line leaving the valves separated from the columella. Length of fruit, 8·5 to 10 mm.; breadth, 4 to 5·75 mm.

REMARKS AND AFFINITIES. Numerous specimens in addition to those figured, almost always incomplete above, and some detached valves (cf. V.20071, V.20071*c*, V.20072, V.42166) only two virtually perfect fruits having been seen. The characters are those of *Gordonia* but no such small living species is known, the nearest in size being *G. lasianthus* Linn. (length, 13·5 mm.) from swamps of Mexico and Florida. The genus also occurs in China, the Himalayas, Ceylon, Further India and the East Indies.

Gordonia truncata Chandler

1926. *Gordonia truncata* Chandler, p. 35, pl. 6, fig. 4*a*, *b*; text-fig. 17.

DIAGNOSIS. Fruit ovoid not as conspicuously attenuated to the apex as is *G. minima*. Base truncate by the large scar of attachment which is much broader than in *G. minima*. Sutures of valves smooth externally not ridged. Length of fruit, 9 mm.; diameter (compressed), 3·5 by 5·5 mm.

HOLOTYPE. Brit. Mus. (N.H.), No. V.20073.

REMARKS. Seven additional fruit bases (V.42167) have now been recognized by the great breadth of the scar of attachment. For a discussion of the relationship of the species see Chandler (1926 : 35).

Section TAONABEAE

Genus ***EURYA*** Thunb.

Eurya becktonensis n. sp.

(Pl. 28, fig. 103)

DIAGNOSIS. Seed transversely oval in outline with reniform cavity (inferred from form and pitting) the micropylar limb apparently broader at its end than the other. Hilum marginal somewhat nearer to the micropylar than to the chalazal limb. Testa thickened laterally near the hilum by a conspicuous patch of coarsely pitted tissue. Dimensions of seed, 2 by 1·25 mm.

HOLOTYPE. Brit. Mus. (N.H.), No. V.42168.

DESCRIPTION. *Seed:* Bisymmetric, transversely oval in outline (dorsal margin slightly imperfect), inflated. Cavity (as inferred from form and pitting) reniform the micropylar limb being slightly broader at its extremity than the other. Hilum an elongate-oval depression on the broad margin between the limbs. Micropyle near one end of the same margin terminating the broad limb and indicated superficially by a point around which the surface pits are small and radially aligned.

Around the hilum (seen on one well preserved surface of the seed) is a thick, coarsely pitted, triangular patch of tissue the inner point of the triangle lying nearer to the chalaza than to the micropylar limb. Pits on the thickened area mostly equiaxial and from 0·057 to 0·1 mm. in diameter. Whole surface of testa deeply and coarsely pitted, the rows of pits lying parallel with the dorsal margin of the seed and with the curvature of the seed cavity. Over the middle part of the curve there are six or seven very regular rows of pits the largest about 0·1 by 0·076 mm. in diameter. Many of the pits are elongate radially. Over the chalazal limb the pits become long and narrow and on its ventral side their walls are scarcely prominent perhaps because only in this part of the testa is the outer wall of the pit preserved obscuring the cavity usually exposed elsewhere by the collapse and abrasion of this wall. Maximum diameter of seed in plane of symmetry, 2 mm. ; diameter at right angles to it, 1·25 mm. ; thickness at right angles to plane of symmetry, 0·75 mm.

REMARKS. One seed only of which the details of structure are clearly preserved on one surface but obscured by the poorer preservation on the other.

The size and form of the pitted seed with its reniform cavity place it in the Taonabeae a section of the Theaceae comprising trees and shrubs. A similar reniform cavity has been seen in *Eurya* and *Adinandra* but the fossil more resembles the thinner-walled *Eurya* than the latter genus. In *Eurya*, however, there appears to be considerable variation in the form of the seed cavity in different species which suggests that there may be some confusion among the living herbarium material of which unfortunately only a very limited amount could be dissected. Thus *E. japonica* R. D. Oldham No. 92 Nagasaki with seeds about 1·2 by 1·5 and 1 by 1·5 mm. in diameter has a reniform seed cavity closely comparable with that of the fossil whereas *E. japonica* var. *nitida* Dyer from West Borneo, Mondi 267, has a hooked cavity with one long and one short limb and is unlike the fossil. *E. japonica* ranges from Japan, China and the East Indies to the Indian Archipelago while allied species (section *Proteurya*) are found in the Sandwich Islands, Malaya and Ceylon. The seed has been named *Eurya becktonensis*.

Genus ***CAMPYLOSPERMUM*** Chandler, 1925 : 16

Campylospermum hordwellense Chandler

(Pl. 28, figs. 104–107)

1925. *Campylospermum hordwellense* Chandler, p. 16, pl. 1, fig. 6*a–c* ; text-fig. 4.

DIAGNOSIS. Fruit with five to eight (or more?) radially arranged seeds in a single row pendulous from an axile apical placenta. Length of fruit about 4 to 5 mm. Seeds bisymmetric, flattened, oblong or oboval in outline, splitting in the plane of symmetry with U-shaped cavity having very unequal limbs. Condyle between limbs occupied by long raphe canal from about one-quarter to one-half the length of the seed. Testa formed externally of coarse inflated cells, internally compact of several layers of small rectangular cells. Seed about 4 mm. long, 1·75 to 2 mm. broad.

HOLOTYPE. Brit. Mus. (N.H.), No. V.20034 (much decayed), Neotype V.20035.

Description. *Fruit:* Globular or subglobular, apex incomplete, base with short stalk (erroneously regarded as style in 1925), lateral walls rarely preserved but showing rounded secreting cells, inner thin layers more frequently seen with remains of longitudinal fibres branching upwards at acute angles. Plurilocular, commonly three-loculed with a single row of five to eight (or more?) pendulous seeds arranged radially around a fibrous axis. Placentation axile, apical. Length of fruit at least 4 mm.; breadth, 3·5 to 5 mm. (without lateral walls).

Seed: Bisymmetric approximately, oblong or oval in outline, laterally flattened by mutual pressure of adjacent seeds in berry, splitting for germination in plane of symmetry, the equal valves showing the U-shaped cavity with U opening upwards with very unequal limbs. The longer micropylar limb lies nearest to the axis of the fruit, the shorter limb carries the subterminal chalaza on its inner angle. Limbs separated by a narrow condyle, hilum marginal at the end of the condyle indicated externally by a small aperture surrounded by radial ridges (cf. Chandler, 1925, pl. 1, fig. 6*a–c* and text-fig. 4). The hilar aperture is situated at about one-third of the length of the seed from its upper margin on the side sloping away from the fruit axis. Raphe canal wide lying within the condyle and extending for about one-quarter to one-half of the length of the seed. Micropyle terminal on the longer limb. Testa about 0·25 to 0·4 mm. thick its outer part (about 0·03 to 0·1 mm. thick) is a layer of large cells much inflated superficially when unabraded or not collapsed. These cells vary in diameter from 0·03 mm. to at least 0·15 mm.; they diverge from the chalazal region over the broad surfaces of the seed (Pl. 28, fig. 106). On the broad surfaces overlying the chalaza is a conspicuous thickening of much inflated large equiaxial cells like those in a similar position in *Eurya becktonensis* (p. 136). Inner part of testa compact formed of several layers of small rectangular cells about 0·016 to 0·025 mm. in diameter as in *Cleyera ? stigmosa* (p. 139). Seed cavity finely striate transversely. Length of seed about 4 mm.; breadth about 1·75 to 2 mm.

Remarks and affinities. The species is very abundant but perfect fruits are scarce owing to the decay and collapse of the lateral walls which allow the seeds to fall free. Examples of four good fruits are in V.42171. Isolated seeds are common (V.20035*a*, V.42172). These specimens were originally referred to the Araceae (Chandler, 1925) but at a later stage the testa structure appeared to connect them with *Cleyera ? stigmosa* then thought to belong to Myrtaceae on account of its U-shaped seed cavity (Chandler, 1961: 80, 108, 335, pl. 8, figs. 8, 9; pl. 11, fig. 18; pl. 34, figs. 16–18). Recent work has however necessitated transferring both fossils to the section Taonabeae of the family Theaceae (Chandler, 1960: 211) where alone the U-shaped cavity is combined with the distinctive testa structure described. No living genus exactly comparable with *Campylospermum* has been seen but there is a close general resemblance to species of *Ternstroemia* and *Anneslea* with a single ring of seeds. So far as the structure in these genera could be observed the testa appears to be smooth and without the large inflated cells described above. It must be borne in mind, however, that very little living material is available for dissection. Hence pending further information the name *Campylospermum* is retained.

Genus *CLEYERA* DC.

Cleyera ? stigmosa (Ludwig)

(Pl. 28, figs. 108–112)

1960. *Cleyera* ? *variabilis* (Chandler) Chandler, pp. 212, 213, 229, pl. 31, figs. 48–56; pl. 34, fig. 145. (see also for earlier references).
1960. *Eurya stigmosa* (Ludwig) Mai, p. 79, pl. 4, figs. 8–17.

DESCRIPTION. Several unmistakable seeds, much decayed or abraded and heavily pyritized show all the specific characters of this widely distributed Eocene species. Two seeds show remains of an outer thin striate coat which somewhat conceals the surface pits normally exposed; it is formed of radially elongate cells, 0·013 to 0·016 mm. broad, which are often elongate-hexagonal in surface view. The descriptions of the species already published are applicable in every detail. There is the same U-shaped cavity and internal condyle, the walls show the same structure superficially, in section they are of the same thickness and are made up of the same small quadrangular cells. The tegmen is transversely striate, formed of equiaxial cells about 0·012 mm. in diameter. Diameter of three seeds respectively: 1·1 by 1·2 mm.; 1·05 by 1·1 mm.; 1·5 by 1·3 mm.

REMARKS. Fourteen seeds (V.42176) and three figured ones. Also known from the Hengistbury and Barton Beds (Chandler, 1960), the Woolwich and Oldhaven Beds, the London Clay (Chandler, 1961) and the Bournemouth Beds, Highcliff Sands and freshwater Bracklesham Beds of Alum Bay (awaiting publication). Mai (1960) described this species from German localities identifying it with *Eurya stigmosa* (Ludwig) after comparison with original material.

Genus *ANNESLEA* Wall.

Anneslea ? costata n. sp.

(Pl. 29, figs. 113–115)

DIAGNOSIS. Seed oboval to narrow-oboval in outline, much compressed having a median slightly curved ridge with rounded inner end over the condyle and a curved rounded ridge over the curved seed cavity beyond which is a marginal rim. Testa fine-celled. Length of seed, 2·2 mm.; breadth, 1·3 to 2 mm.

HOLOTYPE. Brit. Mus.(N.H.), No. V.42177.

DESCRIPTION. *Seed:* Somewhat compressed, oboval to narrow-oboval in outline, curved so that the cavity is U-shaped, the limbs being separated by a condyle which is rounded at the inner end. At the base of the condyle is the marginal hilar aperture leading into the narrow median raphe canal within the condyle. Micropyle possibly represented by a small pit near the hilum at the end of one limb of the cavity. Externally a median slightly curved ridge with rounded inner end overlies the condyle and is separated by a narrow U-shaped furrow from a rounded U-shaped ridge which surrounds it and corresponds with the seed cavity. Outside again is a marginal rim (Pl. 29, fig. 113). Wall of condyle formed of coarse cells.

The external wall of the testa of fine cells the outlines of which are obscure. Seed cavity lined by cells transverse to its length, about 0·012 to 0·016 mm. broad. Length of seed, 2·2 mm.; breadth, 1·3 to 2 mm.; maximum breadth of condyle, 0·5 mm.

REMARKS AND AFFINITIES. Two seeds, one imperfect which was subsequently treated with nitric acid and dissected to show the condyle (V.42178). The character of the U-shaped cavity and raphe canal in condyle indicate the family Theaceae. The seed with its unpitted surface is unlike *Eurya*, *Adinandra* or *Cleyera*. The fine texture of the testa is more suggestive of *Anneslea* or *Ternstroemia*. Bearing in mind that few species of these genera are available for study and that other genera have not been seen at all the species is referred tentatively only to *Anneslea*. The rounded ridges of the surface appear to be distinctive so the name *Anneslea? costata* has been given. The genus *Anneslea* is Indomalayan. *Ternstroemia* belongs to Asia, Africa and South America.

Genus ***HORDWELLIA*** Chandler, 1960 : 228

Hordwellia crassisperma (Chandler)

1926. *Actinidia crassisperma* Chandler, p. 34, pl. 6, fig. 2; text-fig. 15.
1960. *Hordwellia crassisperma* (Chandler) Chandler, p. 229, pl. 34, figs. 140–144.
Hordwellia crassisperma (Chandler) Chandler (in press), pl. 17, figs. 8–61.

The species was referred to Theaceae by Chandler (1960) and has been redescribed and fully illustrated in a monograph on the Dorset Pipe-clay Series (now in press) where range of variation and geological distribution are shown. In addition to the holotype and seeds there illustrated, other seeds from Hordle are V.20069*a* and V.42179.

Family THYMELIACEAE

Genus ?

An obovoid seed slightly imperfect at the pointed micropylar end, originally with crustaceous shining tegmen preserved, now represented by the white sandy cast and pulverized remains of the carbonaceous tegmen (V.42180) found in Bed 10 east of Long Mead End. Length of cast about 5 mm.; breadth, 2·75 mm. The tegmen was columnar in section with straight columns 0·008 to 0·01 mm. broad. A few broken but typical tegmen fragments of other seeds were also seen (V.42181) from Bed 10 east of Beckton Bunny. The surface was shining, formed of equiaxial cells flat or slightly convex superficially, some showing the tiny central lumen, the appearance varying greatly with the degree of abrasion. In some instances the whole surface appears minutely pitted. Most of the fragments show sub-spiral striation or furrowing caused by contraction and curling on drying. Although the material is too incomplete for more definite determination the characters seen indicate Thymeliaceae.

Family LYTHRACEAE

Genus ***MICRODIPTERA*** Chandler, 1957 : 107

Microdiptera parva Chandler

(Pl. 29, figs. 116, 117)

1957. *Microdiptera parva* Chandler, p. 107, pl. 15, figs. 133–149 ; text-fig. 2.

DESCRIPTION. *Seed :* Subquandrangular in outline, much compressed. Raphe prominent median longitudinal on the ventral surface. Wings relatively thick, not concave on the ventral surface but breaking away from the seed body on both sides of the raphe. Dorsal surface with elliptical operculum or germination valve in the lower half of the seed, 0·5 by 0·35 mm. in diameter, ornamented with quadrangular cells in longitudinal rows about 0·03 mm. in diameter. Surface somewhat worn on the dorsal side over the wings, the external coat being abraded so that the underlying striate surface is exposed. The striae swerve around the operculum and across the wings. On the less abraded ventral surface there is a coat of variously oriented convex cells. Length of seed along axis, 0·9 mm. ; total breadth across body and wings, 1 mm.

REMARKS. One seed (V.42182) has been compared with similar seeds from Bovey Tracey and Cliff End, Mudeford. It can be matched exactly in material from these deposits and has therefore been referred to *M. parva.*

Family CORNACEAE

The family is represented at Hordle by six genera, four of which belong to the Mastixioideae (*Eomastixia, Mastixicarpum, Mastixia?* and Genus?) and two to the Cornoideae (*Cornus* and its sub-genus *Dunstania*). Four are extinct.

Section MASTIXIOIDEAE

Genus ***EOMASTIXIA*** Chandler, 1926 : 37

Eomastixia rugosa (Zenker)

1960 *Eomastixia rugosa* (Zenker) : Chandler, p. 234.
Eomastixia rugosa (Zenker) : Chandler (in press), pl. 18, figs. 4–41 ; pl. 19, figs. 1–7.

For references see Chandler Dorset Pipe-clay Flora (in press) where the species is dealt with in detail and its variations and geological range are noted.

One of the most characteristic fossils of Bed 10, east of Beckton Bunny. In addition to the Hordle material recorded in the Dorset Pipe-clay monograph it is represented by the following specimens : V.20079*a* (Chandler, 1926, pl. 6, fig. 6*a*), V.20079*b* (Chandler, 1926, pl. 6, fig. 6*b*), V.20079*c* (Chandler, 1926, pl. 6, fig. 6*d*), V.20079*d* (Chandler, 1926, pl. 6, fig. 6*e*), V.20081 and V.42183 are three-loculed endocarps, V.42184 a four-loculed endocarp (rare), V.20080, V.20082, V.31792, V.42185 numerous endocarps. The original of Chandler, 1926, pl. 6, fig. 6*c* has decayed.

In Germany the species ranges from the Lower to the Middle Oligocene (Kirchheimer, 1957 : 260) whereas in Southern England, so far as present evidence goes, it is confined to the Eocene above the London Clay.

Genus ***MASTIXICARPUM*** Chandler, 1925 : 36

Mastixicarpum crassum Chandler

(Pl. 30, fig. 161)

1960 *Mastixicarpum crassum* Chandler : Chandler, p. 215.
Mastixicarpum crassum Chandler : Chandler (in press), pl. 19, figs. 14–23 ; pl. 20, figs. 1–4.

For references and range of variation of the species as well as its geological distribution see the Dorset Pipe-clay Flora (in press). Like *Eomastixia rugosa* it is among the commonest of the Hordle plants at Bed 10, east of Beckton Bunny and has also been found in an abraded state in rainwash from the contemporary stream channel west of Long Mead End (V.20077).

In addition to the Hordle material to which reference is made in that monograph and above there are the following specimens: V.20075–76, V.20078, V.31791, V.42186. An endocarp (V.42235) alleged to come from the Barton Clay of Barton was found in the Museum after the publication of the Bulletin on the Plant Remains of the Hengistbury and Barton Beds (Chandler, 1960). It is shown here for comparison and in order to complete the records (cf. Pl. 30, fig. 161). It has been fractured transversely and in spite of its poor condition shows the single locule with large longitudinal dorsal infold along the length of which splitting had started.

Genus ***MASTIXIA*** Blume

Mastixia ? glandulosa n. sp.

(Pl. 29, figs. 118–121)

1926. *Carpolithus* sp.2, Chandler, p. 44, pl. 7, fig. 12*a–d* ; text-fig. 28.

Diagnosis. Endocarp fusiform with a longitudinal external groove along which it splits, normally one-loculed, locule C-shaped in transverse section owing to an internal longitudinal infold which corresponds with the external groove. Wall riddled with innumerable resin ducts close to its outer surface. Length of endocarp, 7·75 to 13·5 mm. ; breadth about 3·5 to 5 mm.

Holotype. Brit. Mus. (N.H.), No. V.42187.

Description. *Fruit :* Not seen.

Endocarp : Fusiform sometimes more acutely pointed at one end than at the other, having a median external groove corresponding with a deep longitudinal infold which projects into the single locule causing it to be C-shaped in transverse section. Splitting tends to occur along the groove. External surface where best preserved showing a network of superficial fibres ; when somewhat abraded as is commonly the case, smooth with transverse striae. Walls thick with three regions as seen in transverse section : a thin outer region which tends to peel away on drying ; a thick middle region riddled with innumerable elongate, oval, or irregularly angular lacunae now containing yellow solidified resin ; a thin inner region lining the locule. Locule transversely striate. No germination valve could be detected. Length of endocarp, 7·75 to 13·5 mm. ; breadth, 3·5 to 5 mm. Three typical endocarps showed the following measurements respectively : 1) Length, 10·5 mm. ; transverse diameter, 4 by 3·5 mm. 2) Length, 9·5 mm. ; transverse diameter, 5 mm. 3) Length, 7·75 mm. ; transverse diameter 3·5 mm.

REMARKS AND AFFINITIES. These peculiarly fragile endocarps are liable to shatter as they dry owing to the expansion of the resin in their walls and the contraction on drying of the carbonaceous tissues. Originally described as *Carpolithus* sp. 2 (Chandler, 1926 : 44) and believed to be two-loculed, the two-loculed effect is now known to be due to the close contact of the infold with the ventral wall of the locule caused by compression and partial collapse. At the same time the possibility of two-loculed specimens sometimes occurring cannot be wholly excluded. The single locule with longitudinal infold suggests alliance with *Mastixia* but the evidence of a germination valve is lacking probably because of the ready collapse of the resin riddled walls which makes a valve very difficult to detect. So far these abundant resin cavities have not been seen in *Mastixia* hence the ascription to the genus is regarded as doubtful but it must be borne in mind that only a few species of living *Mastixia* have been examined in section and that in ungerminated and unmacerated *Mastixia* it is almost impossible to detect the valve although longitudinal splitting down the infold is a fairly common feature.

Under the name *Retinomastixia schultei* (Kirchheimer, 1937 : 915, fig. 9) described an endocarp from the Middle Oligocene Brown Coal of Germany which he separated from *Mastixia* because of its numerous secreting cavities and the absence of an external longitudinal furrow associated with splitting. The absence of the furrow also distinguishes *Retinomastixia* from the Hordle fossils although this character can be obscured completely in compressed Hordle material. However *Retinomastixia* appears to differ also in the position of the resin layer which is nearer to the inner surface of the endocarp than in *Mastixia? glandulosa* so that there is a thicker woody layer outside it. *Retinomastixia* is, moreover, described as having a dorsal germination valve. In addition to the material figured from Hordle there are also V.42191 (three endocarps and a few fragments), V.20100, V.20102, V.42192 (various fragments with resin). V.20101 originally figured as *Carpolithus* sp. 2 is now in many fragments.

?Section MASTIXIOIDEAE

Genus?

(Pl. 29, figs. 122–124)

1926. *Carpolithus* sp. 5, Chandler, p. 46, pl. 8, fig. 3*a–d*.

The median infold on each dorsal germination valve of this three-loculed fruit (V.20106*a*) suggests that the specimen may belong to Mastixioideae. Previously no suggestion as to its botanical position could be made. The subglobular shape is one character which distinguishes it from any other species referred to Mastixioideae and the wide external grooving of the dorsal infolds on the valves is another. Also there appears to be no tendency to split along these infolds so far as can be seen.

Section CORNOIDEAE

Genus ***CORNUS*** (Tourn.) L.

Cornus quadrilocularis Chandler

(Pl. 29, figs. 129–133)

1926. *Carpolithus* sp. 4, Chandler, p. 45, pl. 8, fig. 2*a*, *b*.
Cornus quadrilocularis Chandler (in press), pl. 20, figs. 23–26.

DESCRIPTION (emended). *Endocarp:* Subglobular with shallow apical depression but without central canal. Rounded or somewhat pointed at the base, four-loculed each locule having a large dorsal germination valve which separates from the apex downwards but remains attached at the base where it breaks irregularly. External surface finely pitted, walls thick, woody, of regular more or less equiaxial slightly sinuous cells. Locule lining of convex cells with finely digitate walls. Seeds solitary, the testa adhering closely to the locule wall, probably pendulous. Length of original endocarp (V.20106), 3·25 mm.; transverse diameter, 3·5 mm. Length of V.42193, 3 mm.; transverse diameter, 3·8 mm.

Seed: Represented only by collapsed remains of testa showing transversely aligned cells which give rise to transverse striae about 0·008 mm. apart.

REMARKS. The fossil was originally described as *Carpolithus* sp. 4. The finding of a second endocarp made it possible to correct certain errors in the original description. Moreover these specimens are identical with endocarps from the Dorset Pipe-clay Series at Lake which show clearly that the seed was pendulous and confirm the observations recorded above based on Hordle material. A tendency to slight lateral compression is seen in V.42193 as in the Lake endocarps. For further remarks on relationship see Chandler (in press).

Sub-genus ***DUNSTANIA*** Reid & Chandler, 1933 : 459

Dunstania glandulosa (Chandler)

(Pl. 29, figs. 125–128)

1926. *Symplocoides glandulosa* Chandler, p. 41, pl. 7, fig. 5*a*, *b*; text-fig. 26.
1926. *Carpolithes* sp. 3, Chandler, p. 45, pl. 8, fig. 1*a*–*e*.

DIAGNOSIS. Pointed sub-fusiform endocarps about 5 to 9·5 mm. long, two- to four-loculed with small apical depression and ovoid secreting cavities in endocarp wall and to a less degree in septa.

HOLOTYPE. Brit. Mus. (N.H.), No. V.20090 (now much broken), Neotype V.42194.

DESCRIPTION. *Endocarp:* Pointed sub-fusiform, or pointed-ovoid, slightly compressed laterally in some instances, with a small truncation at the apex due to an obconical or basin-shaped depression which may or may not have crenulate margins. Base usually sharply pointed. Locules two to four some of which may be abortive, they communicate with the apical depression. Each locule with a large dorsal germination valve extending almost throughout its length, with smooth sutures except at the base where they break irregularly from the lower part of the endocarp wall. Wall thick formed of cells with sinuous outlines. In section three regions can be distinguished : a thin compact dark outer region, a thick middle region more spongy in texture with numerous ovoid secreting cavities, a thin compact inner layer. Secreting cavities, diameter about 0·1 to 1 mm. with smooth shining walls lined by cells with sinuous outlines often about 0·05 mm. in diameter. The cavities occur in the septa but to a much less extent than in the outer walls of the endocarp, usually smaller in the septa. Locule lining smooth, transversely striate, with sinuous-walled cells. Dimensions of several endocarps : 1) Length, 9·5 mm. ; breadth, 4·25 mm. 2) Length, 8·75 mm. ; breadth, 3·5 mm. 3) Length, 5·5 mm. ; breadth, 4 mm. 4) Length, 9 mm. ; breadth, 8 mm. 5) Length, 7 mm. ; breadth, 2·25 by 3·25 mm. Thickness of dorsal wall where measured, 1·75 to 2·5 mm.

Seed : Solitary, represented only by remains of testa adhering to the locule (N.B. the body described as a seed in 1926, p. 45 was undoubtedly a locule cast). Testa structure obscured owing to crumpling.

REMARKS. When originally described under the names *Symplocoides glandulosa* and *Carpolithes* sp. 3 the structure of these fruits was only partly understood and was therefore wrongly interpreted. The truncate end was then regarded as the base. *Carpolithes* sp. 3 is a well developed endocarp in which the septa has been accidentally pierced so that the three locules have a false appearance of being in communication with one another. Three additional endocarps without septal break were, however, referred tentatively to the same species. In the holotype the base was broken and abraded so that three locule cavities were exposed simulating the apex of an endocarp like *Symplocos*. The examination of hundreds of pyritized fruits of *Dunstania multilocularis* from the London Clay illuminated the structure of the smaller carbonaceous Hordle specimens and it became clear that they and *Dunstania* were closely related. The Hordle endocarps are much smaller than either of the London Clay species, also relatively longer and narrower with more acutely pointed base while so far no more than four locules have been seen. Reid & Chandler referred *Dunstania* to Cornaceae for reasons given (1933 : 461). Kirchheimer has since confirmed the relationship noting that in the sub-genus *Bothrocaryum* of *Cornus* there is a deep depression at the apex of the endocarp and that in the sub-genus *Macrocarpum* and in *Cornus Volkensii* (sub-genus *Afrocrania*) there are secreting cavities. He stresses the fact that the occurrence of more than two locules is not uncommon in living *Cornus* (Kirchheimer, 1948 : 85 ; 1957 : 443). The fossils combine the presence of an apical pit as in *Bothrocaryum* with that of secreting cavities as in *Macrocarpum*. In the latter sub-genus only, a small apical pit sometimes occurs e.g. in *Cornus mas*. The fossils may therefore represent a distinct sub-genus of *Cornus* for which the name *Dunstania* may conveniently be retained at least for the present. The specific name *D. glandulosa* is dictated by its earlier use. In addition to the specimens figured or mentioned above there are the following three-loculed endocarps: V.20103–04*c* (V.20103 being figured Chandler, 1926, pl. 8, fig. 1*a–e*), V.20104*d* a two-loculed endocarp, V.20104*e* a four-loculed endocarp and V.42196 several endocarps, some abraded and some sectioned.

Family ERICACEAE

Section ANDROMEDEAE

Genus? sp. 2

(Pl. 30, fig. 138)

1926. Ericaceae Genus ? sp. 2, Chandler, p. 38, pl. 6, fig. 8*a–c*.

DESCRIPTION. *Fruit:* A superior loculicidal capsule, subcircular in outline, somewhat depressed from apex to base, not stipitate but seated upon a persistent perianth disc equal to the fruit in diameter. Surface of fruit with shallow longitudinal concavities over the septa and slight rounded ridges between these concavities overlying the locules. Apex slightly incurved but having a prominent broad circular style base. External surface finely but irregularly pitted and rugose, formed of equiaxial cells. Carpel wall thick. Placentation axile from large basal placentas in the inner angles of the locules. Seeds numerous sunk partially in shallow depressions of the locule wall. Transverse diameter of fruit originally described (now decayed), 1 mm.; height, 0·9 mm. Transverse diameter of a larger fruit, 1·5 mm.; height, 0·7 mm. Thickness of perianth disc about 0·1 mm.

Seed: Rounded-oblong, anatropous, ornamented with a raised network of elongate longitudinally aligned meshes crossed by fine transverse striae, the meshes following the curvature of the seed at the rounded distal end. Length of seed, 0·33 mm.; breadth, 0·16 mm.

REMARKS. The seeds were beautifully shown in the first described specimen, preserved in shining pyrites which displayed the reticulate pattern very clearly. V.42198 has not dehisced but shows well the external characters of the fruit. V.42199 originally measuring 1 by 0·75 mm. broke longitudinally later and showed three seeds in one locule and their mode of attachment. Reference to the section Andromedeae of Ericaceae was suggested in 1926 and no closer suggestion as to affinity can yet be made. The specimens although somewhat resembling *Epacridicarpum mudense* are distinguished by the depressed form, persistent perianth and several-seeded locules.

Family EPACRIDACEAE

Genus ***EPACRIDICARPUM*** Chandler, 1960 : 214

Epacridicarpum headonense Chandler

(Pl. 29, figs. 134–137)

1926. Andromedeae Genus ? sp. 1, Chandler, p. 37, pl. 6, fig. 7*a, b*.
1960. *Epacridicarpum headonense* Chandler, p. 234, pl. 34, figs. 146, 147,

DESCRIPTION. *Fruit:* A sub-hemispherical or oblate-sphaeroidal five-loculed loculicidal capsule. Upper surface somewhat flattened, lower convex, sometimes slightly stipitate. Surface ornamented with unequal irregular pits. Walls thick the outer layers about 0·05 to 0·15 mm. thick formed of several layers of rounded equiaxial cells many being about 0·025 mm. in diameter; inner layers somewhat thinner of narrow elongate longitudinally aligned cells closely compacted. Locule lining of elongate convex cells which diverge obliquely from subapical axile placentae. These cells vary considerably in length and breadth, many are 0·009 mm. broad and 0·05 to 0·1 mm. long. Length of fruit, 0·55 to 1·25 mm.; diameter 1 to 1·75 mm. (Note in Chandler, 1960, p. 234 the diameter of the species was incorrectly given).

Seed: Pendulous, solitary. Testa too crumpled to show cell structure.

REMARKS AND AFFINITIES. The capsule figured by Chandler (1926, pl. 6, fig. 7*b*) is now represented by two only of its valves. V.20083*a* which was figured by Chandler (1926, pl. 6, fig. 7*a*) and again in this present work and V.20084*a*. In addition there is the beautifully preserved fruit now fractured longitudinally (V.42197, see Pl. 29, figs. 136, 137). V.20084*b* shows two valves of another fruit and V.20084*c*, *d* are valves of doubtful identity. The characters are those of Ericales. Loculicidal dehiscence and slightly sunk apex seen in Clethraceae, Pyrolaceae, Ericaceae and Epacridaceae. Clethraceae are three-loculed. Pyrolaceae and Ericaceae of this type have much larger capsules with thin walls and usually with numerous seeds. The Stypheliae of the family Epacridaceae appear most to resemble the fossil. The locules are single-seeded. Although the dry multilocular "stone" does not appear to dehisce there can be little doubt that maceration prior to germination causes splitting for the release of the seeds. Although the Epacridaceae are chiefly Australian they also grow in India, South America and the sandy heaths of the Malay Peninsula. The fossil species also occurs in the Lower Bartonian and the Highcliff Sands at Cliff End near Mudeford.

Family EBENACEAE

Genus ***DIOSPYROS*** Linnaeus

Diospyros headonensis nom. nov.

1926. *Diospyros antiqua* Chandler, p. 38, pl. 7, fig. 2; text-figs. 21, 22.
Diospyros headonensis Chandler: Chandler (in press), pl. 20, figs. 28, 29; pl. 21, figs. 1–5.

REMARKS. For additional details see Chandler (in press) where a specimen from the Lower Bagshot, Lake, Dorset, with a young fruit was described and illustrated in addition to further Hordle material. Respective registered numbers are also shown there. It may now be added that the calyx is occasionally five-partite (one of the calyces in V.42200) and the range of variation of size is greater than hitherto recorded (cf. V.42201). Several small specimens from Hordle, probably immature, are only about 2 mm. long as against the normal 4·5 to 6·5 mm. In a few cases the sepals have incurled edges giving a deceptive narrow-pointed form. V.20086*d* shows detached sepals.

The name *Diospyros antiqua* is pre-occupied by Watelet (1866: 207) for a leaf impression from the Eocene of Belleu, Paris Basin, France and the Hordle fruits have therefore been given the new name *Diospyros headonensis*.

Family SYMPLOCACEAE

Genus ***SYMPLOCOS*** Jacquin

Symplocos headonensis Chandler

(Pl. 30, figs. 139, 140)

1926. *Symplocos headonensis* Chandler, p. 40, pl. 7, fig. 3*a–c* ; text-fig. 24.
1957 *Symplocos headonensis* Chandler : Chandler, p. 117, pl. 17, figs. 187, 188.
1960 ? *Symplocos headonensis* Chandler : Chandler, p. 215, pl. 31, figs. 58, 59.
Symplocos headonensis Chandler : Chandler (in press), pl. 21, figs. 19, ? 20.

DIAGNOSIS. Endocarp truncate subglobular, ovoid or urceolate, three-to-five-loculed ; external surface smooth formed of fine equiaxial cells. Length, 5 to 6 mm. ; breadth, 3·5 to 5·5 mm.

NEOTYPE. Brit. Mus. (N.H.), No. V.42202.

REMARKS. The smooth external surface of the endocarp is formed of equiaxial cells 0·016 to 0·025 mm. in diameter and the external carpel wall may be as much as 0·4 to 0·45 mm. thick at the middle. For relationship to living species see Chandler (1926 : 40). The originals of Chandler, 1926, pl. 7, fig. 3*a*, *c* are now decayed while that of fig. 3*b* (V.20087) is in poor condition. Hence the selection of a neotype from fresh material. Numerous endocarps are still extant (V.42204).

Symplocos sp.

1926. *Symplocos* sp. 2, Chandler, p. 40, pl. 7, fig. 4 ; text-fig. 25.
Symplocos sp. Chandler (in press), pl. 21, figs. 21, 22.

Although no further material has been found at Hordle, a specimen is known from the Dorset Pipe-clay Series. The small apical depression and smooth external surface appear to be constant features but the evidence does not seem sufficiently distinctive for specific diagnosis. The original endocarp from Hordle (V.20088) is now much broken but shows remains of two seeds extracted from it (V.20089).

Family STYRACACEAE

Genus ***STYRAX*** (Tourn.) L.

Styrax elegans Chandler

1926. *Styrax elegans* Chandler, p. 41, pl. 7, fig. 6*a–f*.
Styrax elegans Chandler : Chandler (in press), pl. 21, figs. 24–28.

The holotype (V.20091) was illustrated by Chandler (1926, pl. 7, fig. 6*a–c* ; in press, pl. 21, figs. 26, 27). The specimen represented in 1926, pl. 7, fig. 6*d* is now decayed. V.20092 was illustrated in 1926 in pl. 7, fig. 6*e* to show the internal nerves of the testa. Broken endocarps somewhat decayed are preserved in V.20093–94, V.42205–06. The latter shows a seed with one concave surface owing to pressure of a second seed in the fruit during growth. The discovery of the species in the Dorset Pipe-clay Series at Lake may be noted.

Family OLEACEAE

Genus ***OLEA*** (Tourn.) L.

Olea headonensis n. sp.

(Pl. 30, figs. 141–143)

1926. Oleaceae Genus ?, Chandler, p. 42, pl. 7, fig. 7 ; text-fig. 27*a–c*.

DIAGNOSIS. Endocarp subovoid but with slight bisymmetry, two-loculed, one locule being abortive, dehiscing loculicidally. External surface smooth or slightly rugose. Length of endocarp, 3·25 to 5·5 mm. ; breadth in plane of symmetry, 2·25 to 4·25 mm. ; thickness, 2 to 3·5 mm.

HOLOTYPE. Brit. Mus. (N.H.), No. V.42207.

DESCRIPTION. *Endocarp :* Woody, subovoid but slightly bisymmetric, angled at the apical end in the plane of symmetry, dehiscing into equal valves loculicidally, two-loculed, one locule being abortive, having one developed pendulous seed in the mature locule. Attachment scar large, basal, leading into a short oblique fibro-vascular canal (Pl. 30, figs. 142, 143 and Chandler, 1926, text-fig. 27*b*) which lies in the plane of dehiscence. External surface smooth, or only slightly rugose, usually without fibres although occasional fibre impressions are seen. Locule lining transversely striate and puckered, shining, with underlying transverse fibres. Smooth suture for dehiscence showing fine fibres variously aligned. Dimensions of four endocarps : 1) Length, 4·75 mm. ; breadth, 3·75 mm. ; thickness, 3 mm. ; thickness of wall, 0·8 mm. 2) Length, 3·75 mm. ; breadth, 2·75 mm. ; thickness, 2·5 mm. 3) Length, 5·5 mm. ; breadth, 4·25 mm. ; thickness, 3·5 mm. 4) Length, 3·25 mm. ; breadth, 2·25 mm. ; thickness, 2 mm.

Seed : Much crumpled as preserved. Testa formed of double-walled rectangular cells frequently measuring 0·1 by 0·05 mm. The seed shows remains of dark-coloured broad flat fibre bands (now much shattered).

REMARKS AND AFFINITIES. Perfect endocarps are V.42208, V.42210. There are also an endocarp split loculicidally (V.42211) and numerous fragments (V.42212). V.42209 was figured by Chandler, (1926, pl. 7, fig. 7 ; text-fig. 27*a–c*). Form, locules, dehiscence and funicle, also the structure of endocarp and seed suggest Olacineae, family Oleaceae. No Recent *Olea* has been seen without external fibres associated with marked rugosities. Their absence in the fossil is no doubt due to abrasion as in some species of *Olea* they are readlly removable and traces of them have been seen in *O. headonensis*. Endocarps similiar in form and size are found in the living genus *Olea* which today occurs in the Mediterranean, South Africa, the East Indies, Polynesia and Australia.

Family BORAGINACEAE

Genus ***OMPHALODES*** Tourn. ex Moench.

Omphalodes platycarpa Chandler

1926. *Omphalodes platycarpa* Chandler, p. 42, pl. 7, fig. 8*a*, *b*.

HOLOTYPE. Brit. Mus. (N.H.), No. V.20095.

REMARKS. The original of Chandler, 1926, pl. 7, fig. 8*b* is decayed. V.20095*a* is a carpel partially dissected to show the inner surface (figured Chandler, 1926, pl. 7, fig. 8*a*). Additional material is needed to confirm the determination.

Family ACANTHACEAE

Genus *ACANTHUS* Linnaeus

? *Acanthus* sp.

(Pl. 30, figs. 144, 145)

DESCRIPTION. *Seed:* Much compressed, more or less quadrangular in outline, the angles being somewhat rounded. Two of the adjacent sides of the quadrangle are of approximately equal length and are appreciably shorter than the other two. A large elliptical marginal scar is seen at the middle of one of the shorter sides, this side being concave. The other short side is slightly convex. Unfortunately the angle where the two longer sides meet is broken. One broad surface of the seed is more or less flat, the other is concave near the hilar scar but has a long narrow curved facet extending from the angle where the two shorter sides meet to that where the two longer sides meet. It is probably caused by pressure of an adjacent seed or by contact with the fruit wall during growth. Surface ornamented all over with close-set puckerings many of which appear as shining black convex areas with toothed outlines. These areas may be circular, elliptical or irregular and are about 0·05 to 0·1 mm. in diameter. In general the surface is rough owing to fine equiaxial pits but a few of the black convex puckerings do not show the pitted tissue seen elsewhere. Along a line between the broken angle of the seed and the hilum the puckerings become somewhat elongate. Maximum diameter of seed, 4 mm.; diameter at right angles to this, 3 mm.; thickness at right angles to the broad surfaces, 1 to 1·5 mm.

REMARKS. The form and puckered surface suggest Acanthaceae. The fossil most resembles a few seeds in the Reid Collection found as accidental impurities in a packet of *Acacia catechu* from an Indian Collection of seeds presented by the Keeper of Kew Herbarium. These were provisionally identified as *Acanthus* sp.

Family CAPRIFOLIACEAE

Genus *SAMBUCUS* (Tourn.) L.

Sambucus parvulus Chandler

1926. *Sambucus parvulus* Chandler, p. 43, pl. 7, fig. 9*a–c*.
Sambucus parvulus Chandler: Chandler (in press), pl. 23, figs. 1–10.

DIAGNOSIS. Seed 1·1 to 1·5 mm. long. Surface with about six to ten sinuous transverse ridges with interspaces as broad as or broader than the ridges.

HOLOTYPE. Brit. Mus. (N.H.), No. V.20096.

DESCRIPTION. The original description has been emended in minor respects and now stands as follows: Seed exceptionally small and thin, obovate or elongate-obovate, compressed, often concavo-convex, anatropous, micropyle and hilum terminal on the ventral face ; raphe ventral median longitudinal marked externally by an obscure longitudinal angle. Surface ornamented with from six to ten sinuous, sometimes interrupted transverse ridges with interspaces as broad as or broader than the ridges. Testa formed externally of equiaxial cells about 0·012 to 0·016 mm. in diameter. Length of seed, 1·1 to 1·5 mm. ; breadth, 0·6 to 1 mm.

REMARKS. Although the majority of the seeds were found in Bed 10 east of Beckton Bunny, a few occurred in Bed 10 below Hordle House. The well represented seeds are readily distinguished by their small size and delicate appearance from any living *Sambucus* seed. The wide spacing and relative coarseness and fewness of the transverse ridges is a distinctive feature. A single seed was found in the Dorset Pipe-clay Series at Lake. Although primarily a temperate genus of the Northern Hemisphere it also occurs in the East Indies, Australia, Tasmania and South America. In addition to specimens figured there are numerous seeds (V.42214).

Family CUCURBITACEAE

Genus ***CUCURBITOSPERMUM*** Chesters, 1957 : 56

Cucurbitospermum reidii n. sp.

(Pl. 30, fig. 146)

1926. Cucurbitaceae Genus ?, Chandler, p. 43, pl. 7, fig. 10*a*, *b*.

DIAGNOSIS. Seed subtriangular in outline, elongate and narrow at the base, truncate at the apex, with a raised somewhat rugose median area pointed at both ends and a flat smooth marginal area which disappears at the apex, ends abruptly at the base and corresponds with an internal suture. Length of valve, 8·5 mm. ; breadth, 4·5 mm.

HOLOTYPE. Brit. Mus. (N.H.), No. V.20098.

DESCRIPTION. *Seed :* Subtriangular in outline, elongate and narrow at the base, truncate at the apex, flattened, with a raised ornamental median area which is pointed at both ends. The ornamentation is of elongate rugosites aligned more or less at right angles to the margin of the raised area. There is a broad smooth flat marginal rim which does not extend around base or apex ; at the apex its termination causes the truncate appearance. At the base also it ends abruptly. Hence at both ends of the seed the pointed extremities of the raised median area project beyond the rim. An internal hollow corresponds to the raised area and a marginal internal suture to the external smooth rim (Chandler, 1926, pl. 7, fig. 10*a*, *b*). The broad suture indicates that the specimen is one valve of a bisymmetric seed which has split marginally in the plane of symmetry, the other valve is missing. Length of valve, 8·5 mm. ; breadth, 4·5 mm.

REMARKS AND AFFINITIES. A single seed from Bed 10 below Hordle House. Both apex and base of this seed are very slightly imperfect, and the specimen is abraded so that the micropyle and raphe are obscure but form and structure indicate Cucurbitaceae. The seed is of a distinctive form which has not been matched precisely among the living genera that could be examined. Hence the reference to the form-genus *Cucurbitospermum*. A similar raised median area occurs in *Sicydium* Schlechtd. a tropical American genus, otherwise not closely similar, and in *Lagenaria* Ser. the median area is of the same shape but is not conspicuously raised and rugose as in the fossil.

Family ?

Genus ***RHAMNOSPERMUM*** Chandler, 1925 : 30

Rhamnospermum bilobatum Chandler

1960. *Rhamnospermum bilobatum* Chandler : Chandler, pp. 216, 236, pl. 32, figs. 60, 61 ; pl. 35, figs. 155, 156.

Rhamnospermum bilobatum Chandler : Chandler (in press), pl. 23, figs. 18–38, pl. 24, figs. 1–9. See also for earlier references.

The species occurs abundantly at Hordle in Bed 10, east of Beckton Bunny (V.42216) and below Hordle House (V.42215) and is rare in Bed 29 (V.20047*a*). In addition to the above there are V.20064*a* (Chandler, 1926, pl. 5, fig. 1*a*), V.20064*b* (Chandler, 1926, pl. 5, fig. 1*b* ; Chandler (in press), pl. 23, fig. 18) and V.20064*c* (Chandler, 1926, pl. 5, fig. 1*c* ; Chandler (in press) pl. 23, fig. 19).

For range of species and its variations, also remarks on affinities see Chandler, Flora of the Dorset Pipe-clay Series (in press).

Carpolithus fibrosus n. sp.

1926. *Carpolithus* sp. 7, Chandler, p. 46, pl. 8, fig. 5*a*, *b* ; text-fig. 30.

Diagnosis. Fruit syncarpous, two to six-carpelled, seated on a low conical receptacle with free persistent sepals, obovoid or ovoid, splitting loculicidally. Endocarp thick and woody formed of stout longitudinal fibres. Length of fruit, 4·25 to 6 mm. ; breadth, 3·25 to 4·5 mm. Seeds linear, anatropous, about 2 to 3 mm. long with hyaline integuments.

Holotype. Brit. Mus. (N.H.), No. V.20108.

Description. *Fruit :* Syncarpous, woody, ovoid or obovoid, superior, attached to a low conical receptacle which bears at its margin a small calyx of persistent free sepals. (Both calyx and receptacle often broken away as in holotype, see Chandler, 1926, pl. 8, fig. 5*a*.) Two to six-carpelled, splitting loculicidally especially at the apex but the smooth surfaces of the septa rarely seen except towards the base. Interior of fruit occupied almost completely by longitudinally aligned agglomerated woody fibres (endocarp?) among which slender pendulous seeds lie in elongate narrow cavities. Whether there is more than one seed in a cavity has not been determined. External surface rough, exocarp about 0·2 mm. thick formed of shining, longitudinally aligned cells of irregular shape about 0·03 mm. in diameter. There are a few embedded longitudinal fibres in this coat, one such delimiting the margin of each carpel. Internally each carpel has a conspicuous median longitudinal ridge formed of woody fibres especially noticeable at the apex where the fibres are somewhat contorted and appear to form placentas. Length of fruit, 4·25 to 6 mm. ; diameter, 3·25 to 4·5 mm.

Seed: Linear, compressed or inflated, anatropous. Hilar surface flat, oval; chalaza a black oval thickened scar 0·35 by 0·25 mm. in diameter at the opposite end to the hilum situated therefore at the end of the seed near the base of the locule. Integuments thin. The coat usually preserved (tegmen?) is hyaline formed of longitudinally elongate parallel-sided cells 0·012 mm. broad, square or facetted at the ends. Outside this a rough coat is sometimes seen with similiar cells and there is sometimes a coat of equiaxial cells about 0·01 to 0·016 mm. in diameter (Chandler, 1926, text-fig. 30*a*) which may be part of the testa, or may belong to the locule wall. Sometimes the hyaline integument bears internal impressions of large rectangular cells 0·016 to 0·025 mm. in diameter. Transversely elongate cells arranged in longitudinal rows have also been seen internally (Chandler, 1926, text-fig. 30*b*). Length of seed, 2 to 3 mm.

REMARKS. Fruits common but often imperfect owing to the tendency to break longitudinally again and again. V.20109*c* is an imperfect fruit with remains of receptacle still attached. V.20109 and V.20109*a* are longitudinally fractured fruits. V.42219 has the pericarp abraded so that the fibre mass is exposed with some seeds showing through it and V.42220 is a similar specimen. Woody interior is well shown in V.42218. In V.42217 half of a longitudinally fractured fruit shows seeds one with a black oval chalazal scar. Other specimens or segments of fruits are V.20109, V.42221–23. The original of Chandler, 1926, pl. 8, fig. 5*b* is decayed. The botanical position has not yet been determined but this readily recognizable species appears to be worthy of a specific name especially as it has now been found also in the Bournemouth Beds. There is a certain resemblance between this and the specimen from the London Clay called *Trochodendron? pauciseminum* (Reid & Chandler, 1933 : 155, pl. 3, figs. 29–33) but that was thought to be septicidal. If further London Clay material could be found a comparison should be made, observations checked and the relationship reconsidered. The size is similar as are the coats of the slender seed.

Carpolithus apocyniformis n. sp.

(Pl. 30, figs. 147, 148)

DIAGNOSIS. Detached valves of a loculicidal multilocular capsule, narrow-ovate in outline, slightly convex on the external surface which is finely furrowed and longitudinally striate, slightly concave on the inner surface which has a median longitudinal septal ridge throughout. Length of valves about 4·25 to 6·5 mm.; breadth about 1·5 to 3 mm.

HOLOTYPE. Brit. Mus. (N.H.), No. V.42224.

DESCRIPTION. *Valve:* Apparently part of a multilocular capsule now always detached, narrow-ovate in outline, pointed or rounded at the distal end (usually broken), truncate at the proximal end where broken from the fruit. External surface slightly convex, black and rather rough owing to short irregular longitudinal furrows, cell structure obscure but some cells with black shining contents can be seen. Inner surface slightly concave, smooth finely striate longitudinally with low median longitudinal ridge throughout its length which appears to be the remains of a septum. Beneath the epicarp is a light brown layer formed of cells about 0·012 mm. long, 0·016 mm. broad. The valve is solid as seen in transverse section. Length of valve about 4·25 to 6·5 mm.; breadth, 1·5 to 3 mm.

REMARKS. These specimens are not uncommon and two have occasionally been seen adhering by their lateral margins. The solid section excludes all possibility that they are seeds in spite of a superficial resemblance to seeds of Apocynaceae. The adherent specimens, the constant presence of the median ridge and the transverse break at one end suggests that they are detached valves of a dehisced capsule but no suggestion as to relationship can at present be made. The distal end of the holotype is imperfect but the form of the unbroken valve tip has been seen on a broken specimen with other imperfect valves in V.42226. There is also an almost perfect tip in V.42227 and in the figured specimen V.42225 (somewhat pyritized). Further material will be described in due course when the British Museum monograph on the Bournemouth Beds is published.

Carpolithus sp.

(Pl. 30, figs. 149–153)

1926. *Carpolithus* sp. 8, Chandler, p. 47; text-fig. 31.

DESCRIPTION. *Ovary:* Superior, conical with flat pentagonal basal perianth disc showing remains of peduncle. Carpels normally three (rarely four), syncarpous with three short apical styles and three locules. Epicarp thin, loosely fitting, shining, formed of square or hexagonal cells, carpel wall within spongy in transverse section. Locule lining of transversely elongate cells arranged in vertical rows, longitudinally puckered the puckerings sometimes branching and anastomozing. Seeds not seen. Length of ovary about 3 mm.; breadth, 1·75 to 2·5 mm.

REMARKS. These specimens seem to be immature fruits or ovaries rather than ripe fruits. They are often collapsed and distorted. The relationship has not been discovered. The following are three-loculed: V.20110, V.20110*a* (Pl. 30, fig. 151), V.20110*b* (Pl. 30, fig. 150, shows perianth disc clearly), V.20110*c* (Pl. 30, fig. 149), V.20110*d* (Pl. 30, fig. 153). V.20110*e* (Pl. 30, fig. 152) is a rare four-loculed specimen. Numerous fruits are registered under V.42228.

? ***Carpolithus gardneri*** Chandler

1926. *Orites* sp. Chandler, p. 47, pl. 8, fig. 6.

V.15520 the finest specimen was originally described as *Orites* sp. There are in addition nineteen other specimens V.421*a–s*. All are now much decayed. Some are merely detached fruits. One internal cast shows fine transverse striations. As noted in 1926 there is a resemblance to a species from the Reading Beds now described as *Carpolithus gardneri* (Chandler, 1961: 85, pl. 9, figs. 1–5; text-fig. 4) both in the branching racemose habit and structure of the pods but *C. gardneri* appears to have more slender fruits and it is doubtful whether the two are identical or whether there is sufficient evidence to connect the Hordle species with *Orites* in spite of a similarity of habit. The specimens are preserved in a sandy whitish-grey clay. The locality in Hordle cliff is almost certainly Bed 10 as the matrix agrees with that of "*Nelumbium buchi* Ett." (Chandler, 1926 : 48).

Carpolithus sp.

(Pl. 30, figs. 154–156)

1926. *Carpolithus* sp. 1, Chandler, p. 44, pl. 7, fig. 11*a*, *b*.

This six-lobed solid organ is still unidentified. Each of the six lobes has two transverse constrictions and new material shows remains of a shining epidermis of equiaxial cells. The comparable Recent object found as described in 1926 as an impurity in a packet of seed of *Zelkova Keaki* from the Yokohama Nursery Company is figured in Pl. 30, fig. 157. Length of specimens, 3 to 6 mm. ; transverse diameter, 1 to 3·5 mm. V.42229 (see Pl. 30, figs. 155, 156) and V.42230–31 are extant but the specimen figured in 1926 is now decayed.

Carpolithus sp.

(Pl. 30, fig. 158)

DESCRIPTION. *Seed :* Small, bisymmetric, curved, reniform represented by one valve only. Hilum near the middle of the concave margin. Other organs obscure but as one limb is narrower than the other the micropyle probably lay at its tip. Hilum a conspicuous aperture leading directly to the seed cavity. As seen in section the wall of the chalazal limb somewhat overlaps the wall of the micropylar limb and is recurved lying closely upon itself and passing into the tegmen. Testa surface of equiaxial cells superficially which diverge from the hilum, are about 0·012 to 0·016 mm. in diameter, and are so thick-walled that the small cavity appears as a central pit or depression. In section the testa is columnar and about 0·05 mm. thick. Lining of testa obscure but apparently formed of digitate cells. Maximum diameter of seed about 1·15 mm. ; diameter through the hilum at right angles to this about 0·9 mm. The seed has split in the plane of symmetry as for germination. Its systematic position is not known.

Carpolithus sp.

(Pl. 30, fig. 159)

DESCRIPTION. *Fruit :* Subglobular, syncarpous, four-loculed, locules unequally developed, opening by dorsal valves which gape at the apex and sides but break irregularly below. No central canal seen but there appears to be a thickened scar on the median line of the ventral wall of each locule at about one-quarter of the length from the apex which may mark the attachment of a solitary seed. Walls woody, septa formed internally of equiaxial cells about 0·016 mm. in diameter, but superficially of elongate cells parallel with the surfaces, the length of these cells being about 0·05 mm. and their breadth about 0·008 mm. Cells of the locules elongate, about 0·007 mm. broad and of variable length, frequently 0·05 mm. These cells are arranged in groups on the whole obliquely aligned and diverging from the subapical placenta (?) and below this point upwards from the median ventral line of the locule.

Seed : Agreeing with the locule in shape, with large thickened basal chalaza ; testa of longitudinally elongate cells, 0·01 mm. broad.

REMARKS. A single fruit of unknown affinity now dissected.

Gall or Tuber?

(Pl. 30, fig. 160)

DESCRIPTION. A subglobular hollow body, burst at one end (now fractured into two pieces) with scaly surface having irregular rugosities separated by deep cracks sometimes arranged concentrically around a more or less smooth area. There are a few small circular apertures seen especially on the smooth areas. Wall finely columnar in section and about 0·05 mm. thick. Within are remains of a yellow semi-translucent skin of chitinous appearance in which no cell walls can be seen. Dimensions, 2·5 by 2 mm.

REMARKS. A gall or tuber? which closely resembles similar organisms from the Dorset Pipe-clay Series (Chandler, (in press), pl. 27, figs. 26–29) and from the London Clay (Chandler, 1961 : 324, pl. 32, fig. 33). Identity not determined.

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EXPLANATION OF PLATES

Unless specifically stated otherwise all specimens figured are from Hordle.

PLATE 24

Salvinia mildeana Goeppert

FIG. 1. Part of the leaf (figured Chandler, 1925, pl. 1, fig. 1*a*) to show arrangement of papillae between secondary nerves. ×4. (V.36344.)

Acrostichum lanzaeanum (Visiani)

FIG. 2. Pinnule fragment. ×2. (V.42058.) Alleged to come from Barton clay, Barton. For comparison with Hordle material previously figured.

Potamogeton pygmaeus Chandler

FIGS. 3, 4. Abraded endocarps. In fig. 3 keel tip broken. ×15. (V.42054–55.) *Limnocarpus* Band, Colwell Bay, Isle of Wight.

FIGS. 5, 6. Endocarps from Hordle for comparison. Fig. 5 shows gaping keel, fig. 6 the style. ×15. Decayed.

Limnocarpus forbesi (Heer)

FIG. 7. Endocarp, side, with style and lateral foramen; slightly imperfect below. ×15. (V.42064.) *Limnocarpus* Band, Colwell Bay, Isle of Wight.

FIG. 8. Another, similar aspect, tip of keel broken. ×15. (V.42062.) Lower Headon, bomb crater, Downton, Hordle.

FIG. 9. Endocarp, ventral, with style and stalk. ×15. (V.42065.)

FIG. 10. Endocarp, dorsilateral, tilted to show tip of keel. ×15. (V.42066.)

FIG. 11. Endocarp, dorsilateral, sand filled cavity exposed by loss of keel. ×15. (V.42061.)

Figs. 9–11 from *Limnocarpus* Band, Colwell Bay, Isle of Wight.

Stratiotes hantonensis Chandler

FIGS. 12, 13. Inner surface of two valves from sigmoidal seeds showing short raphe. ×6·5. (V.42084, V.42086.)

FIG. 14. Seed somewhat dorsiventrally crushed. ×6·5. (V.42085.)

FIGS. 15, 16. Two seeds showing sigmoidal and hooked forms. ×6·5. (V.42083, V.42086*a*.)

Stratiotes headonensis Chandler

FIG. 17. Typical seed for comparison with the above. ×6. (V.20031*a*.)

Caricoidea minima (Chandler)

FIG. 18. Holotype. Endocarp tilted to show basal aperture and a longitudinal rib. ×15. (V.20033.)

FIG. 19. Fruit, side. ×15. (V.42087.)

FIG. 20. Another endocarp, side. ×15. (Decayed.)

FIG. 21. Larger fruit. ×15. (V.42088.)

Caricoidea obscura Chandler

FIG. 22. Fruit, side. ×15. (V.42092.)

FIGS. 23, 24. Two endocarps. ×15. (V.42093–94.)

Scleria hordwellensis n. sp.

FIG. 25. Holotype. Fruit, apex, calyx can be seen projecting around the circumference. ×6·5. (V.42096.)

FIG. 26. Same, side, at the base is seen thick calyx with transverse puckerings, (*s*) style. ×15.

CYPERACEAE, Genus ?

FIG. 27. Abraded fruit, side, (*s*) style. ×15. (V.42097.)

Spirematospermum headonense n. sp.

FIG. 28. Holotype. Fruit broken at stylar end so that seeds are exposed. ×1 approx. (V.42098.)

FIG. 29. Same with near wall removed to expose more of the seeds. ×1·3.

FIG. 30. Another fruit broken at stylar end from which seeds have fallen. ×1 approx. (V.42099.)

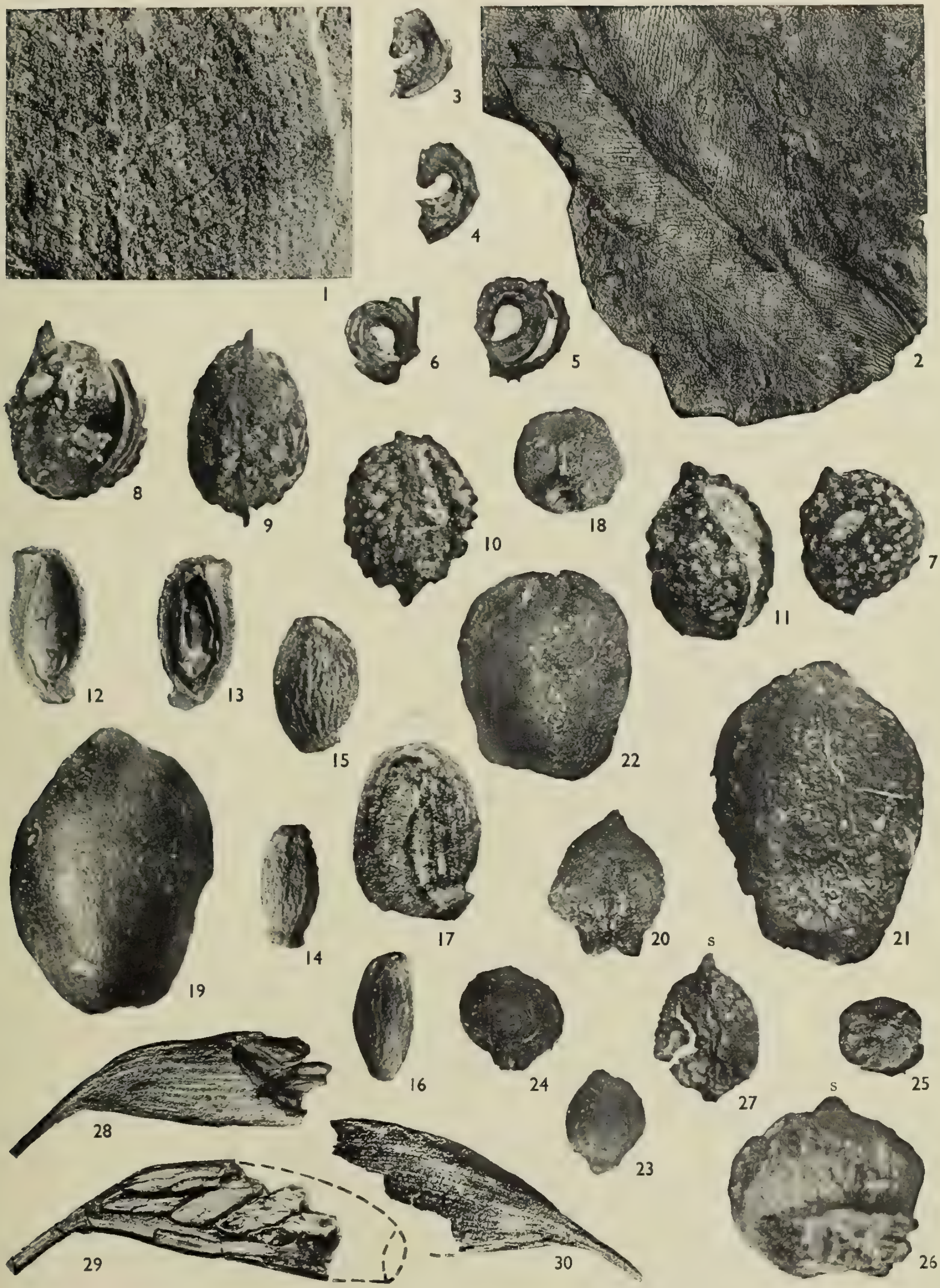
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PLATE 25

Spirematospermum headonense n. sp.

FIG. 31. Seed. ×9. (V.20037.)

FIG. 32. Seed. ×9. (V.42057*a*.) In matted mass of *Acrostichum lanzaeanum* said to come from Barton clay, Barton cliff.

Myrica boveyana (Heer)

FIG. 33. Endocarp abraded surface cracked along basal attachment and placenta. ×6·5. (V.42102.)

FIG. 34. Valve of another, interior showing locule and broad flat marginal suture. ×15. (V.42103.)

Carpinus boveyanus (Heer)

FIG. 35. Abraded fruit, (*b*) basal attachment scar. Longitudinal furrows due to calyx fibres are obscurely seen. ×15. (V.42104.)

Broussonetia rugosa Chandler

FIG. 36. Holotype. Endocarp slightly broken. ×15. (V.20039.)

FIG. 37. Another endocarp. ×15. (V. 20039*b*.)

Moroidea hordwellensis n. sp.

FIG. 38. Holotype. Fruit, side, (*st*) style; (*f*) funicle; (*ch*) position of chalaza within. ×15. (V.42105.)

Becktonia hantonensis n. gen. & sp.

FIG. 39. Holotype. Endocarp, side (bursting below), (*a*) subapical foramen for funicle. ×6·5. (V.42106.)

Hantsia pulchra (Chandler)

FIG. 40. Seed, side showing curvature, (*h*) rimmed hilum. ×15. (V.42107.)

Hantsia glabra n. sp.

FIG. 41. Holotype. Seed, side, smooth surface with finely toothed cells, (*h*) rimmed hilum. ×15. (V.42111.)

FIG. 42. Same, opposite side. Aperture of hilum (*h*) turned towards camera. ×15.

FIG. 43. Slightly distorted seed, (*h*) hilar rim (slightly incomplete). ×15. (V.42110.)

Brasenia oblonga Chandler

FIG. 44. Seed, side, longitudinal raphe on left. Tubercles well shown. ×15. (V.20043*a*.)

FIG. 45. Same, hilar end looking on to aperture from which embryotega has fallen. ×15.

FIG. 46. Holotype. Uncrushed seed. ×15. V.20043.

Palaeosinomenium obliquatum (Chandler)

FIG. 47. Holotype. Endocarp (*s*) stylar limb, elongate foramen (*f*) seen near stylar limb. ×6·5. (V.20049.)

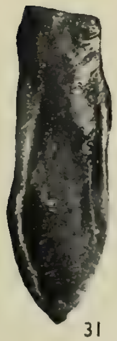
FIGS. 48, 49. Much broken valves of a second endocarp, (*st*) stylar limb. ×6·5. (V.20050.)

FIG. 50. Stylar limb of another endocarp showing ornamentation of marginal flange. ×15. (V.42122.)

LAURACEAE, Genus ?

FIG. 51. Berry, apex (crushed dorsiventally) ×6·5. (V. 42123.)

FIG. 52. Same in longitudinal section showing conical endocarp with columnar wall, mesocarp represented by light coloured pyrites. ×6·5.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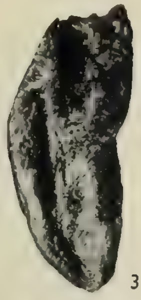
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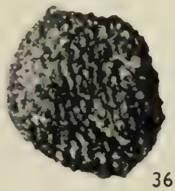
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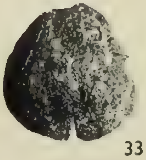
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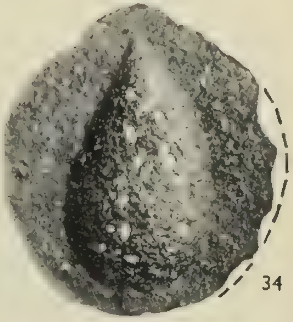
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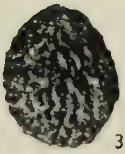
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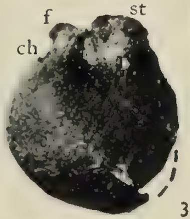

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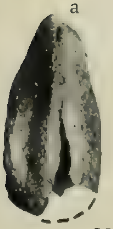

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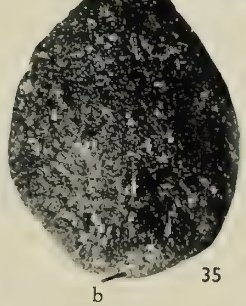

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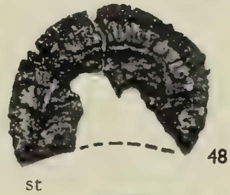

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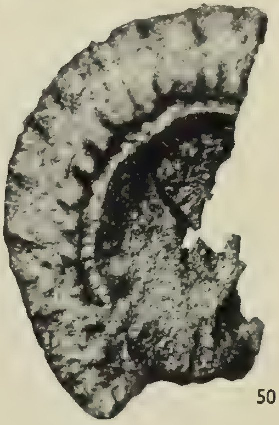
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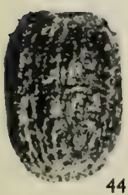
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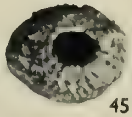
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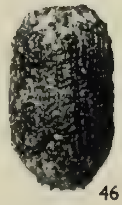
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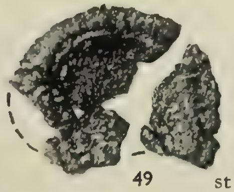

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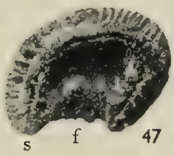

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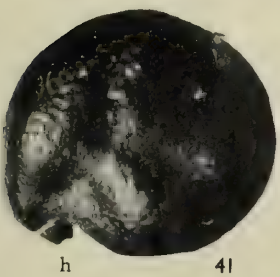

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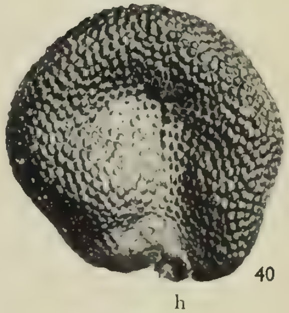

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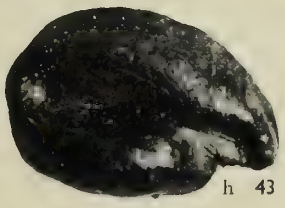

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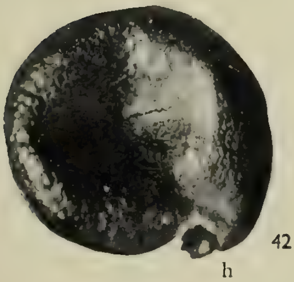

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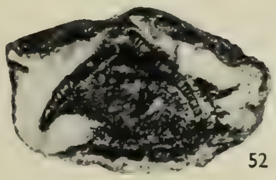
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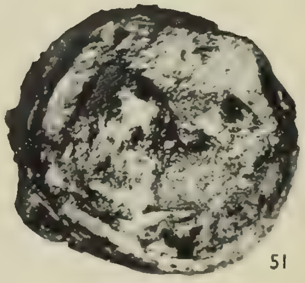
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PLATE 26

Aldrovanda ovata (Chandler)

Fig. 53. Seed showing long hilar neck, mucro at distal end, and longitudinal raphe ridge (on right). ×15. (V.42126.)

Fig. 54. Another with somewhat abraded surface. ×15. (V.42124.)

Fig. 55. Seed in longitudinal section showing prismatic cells within testa. ×15. (V.42125.) Colwell (presumed Lower Headon).

Eoliquidambar hordwellensis n. gen. & sp.

Fig. 56. Holotype. Mature fruiting head, base, showing areoles. ×2·6. (V.42131*a*.)

Fig. 57. Same, different aspect, showing a fruit (*f*) with two crescentic valves in an areole. ×2·6.

Fig. 58. Three areoles of same showing wrinkled shining epidermis over the valves of enclosed fruits, the evidence that they bore no awns. ×6·5.

Fig. 59. Immature fruiting head with areoles enclosing two-valved fruit apices. ×6·5. (V.42131.)

Protoaltingia hantonensis Chandler

Fig. 60. Much abraded fruiting head. ×6. (V.20054.)

LEGUMINOSAE, Genus ?

Fig. 61. Crushed seed. ×6·5. (V.43696.)

Fig. 62. Another genus. Hilum (*h*) associated with tumescent area. ×15. (V.43697.)

Zanthoxylum hordwellense n. sp.

Fig. 63. Holotype. Seed, side. Long hilar scar on right, (*ch*) position of chalaza. ×15. (V.20059.)

Fig. 64. Same, ventral view showing narrow-triangular hilar scar with orifice for raphe at its lower end. ×15.

Zanthoxylum compressum Chandler

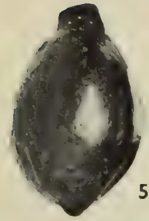
Fig. 65. Holotype. Seed, side, short hilar scar on right. ×6·5. (V.20061.)

Fig. 66. Small area of same showing characteristic surface ornamentation. ×15.

Fig. 67. Another seed with abraded surface and shorter hilar scar (right). (*ch*) indicates position of chalaza. ×6·5. (V.42137.)

Rutaspermum ornatum (Chandler)

Fig. 68. Seed, broken on dorsal side, showing cell structure and surface ornamentation, also smooth area around hilar scar (right). (*ch*) position of chalaza. ×15. (V.42145.)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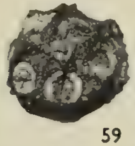
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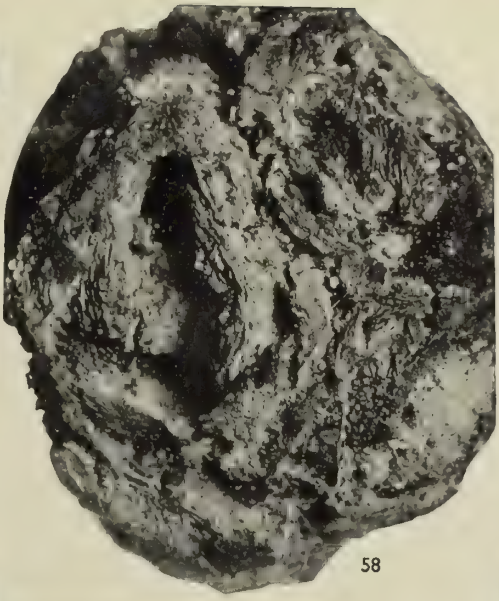
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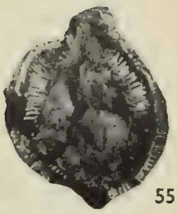
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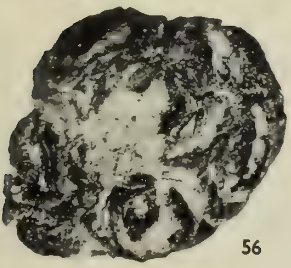
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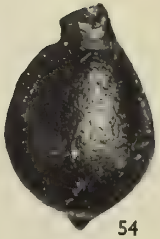
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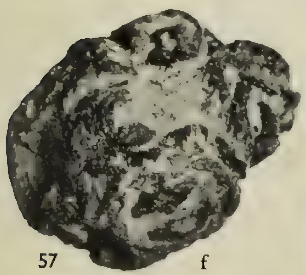
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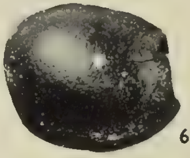
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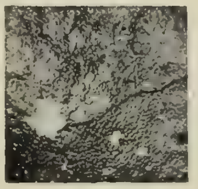
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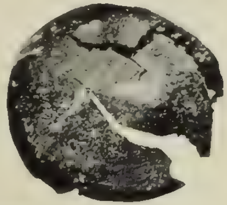
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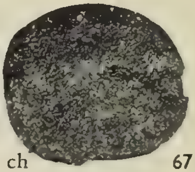
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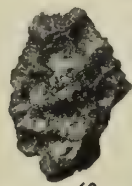
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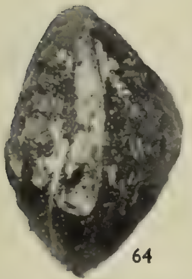
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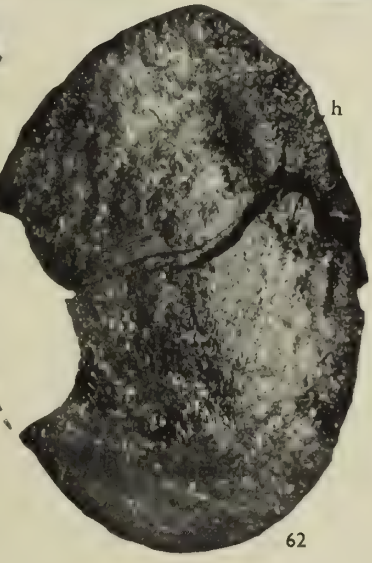
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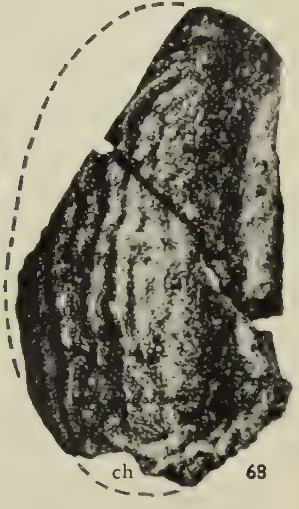
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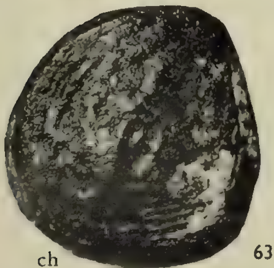
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PLATE 27

Rutaspermum ornatum (Chandler)

FIG. 69. Neotype. Seed, hilar scar to left. ×6·5. (V.42142.)

FIG. 70. Another slightly tilted to show hilar scar on right, smooth area around it clearly seen. ×6·5. (V.42143.)

FIG. 71. Smaller seed, hilar scar to left. ×6·5. (V.42144.)

ANACARDIACEAE SPONDIEAE, Genus ?

FIG. 72. Fragment of fruit showing sac-like, closely packed, secreting cavities exposed by fracture and abrasion. ×15. (Decayed.)

FIG. 73. Another fragment of same. ×15.

Palaeobursera lakensis Chandler

FIG. 74. Endocarp, ventral, (broken on left) showing cell structure. (*p*) Aperture leading to placenta. ×15. (V.42147.)

FIG. 75. Same, dorsal. ×15.

? *Iodes* sp. (or ? *Natsiatum* sp.)

FIG. 76. Funicular margin of an endocarp, (*st*) style. Funicular canal exposed below by a break in its outer wall. ×4. (V.20063.)

FIG. 77. Same, interior, (*p*) placenta. ×4.

Iodes ? *hordwellensis* n. sp.

FIG. 78. Holotype. Endocarp, apex, funicle on left. ×2·8. (V.42153.)

FIG. 79. Same, side, (*st*) style, funicle on left. ×15.

Icacinicarya transversalis n. sp.

FIG. 80. Holotype. Valve of endocarp, exterior (slightly imperfect), funicle on right, (*st*) style. ×2·8. (V.23420.)

FIG. 81. Same, interior, (*st*) style, funicle on left. ×2·8.

FIG. 82. Another distorted endocarp, broken at style (*st*). ×2·8. (V.23419.)

Icacinicarya becktonensis n. sp.

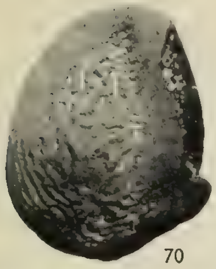
FIG. 83. Holotype. Endocarp, side, abraded at apex, funicle on right. ×6·5. (V.42155.)

FIG. 84. Same, apex, abrasion has exposed circular hilar scar (*s*) on seed within and part of funicle to right of it. ×6·5.

Frangula hordwellensis n. sp.

FIG. 85. Holotype. Pyrene, side, showing median longitudinal angle. (*p*) Fragment of outer pitted coat. Hilum at base. ×6·5. (V.42156.)

FIG. 86. Same, opposite, gently convex surface. ×6·5.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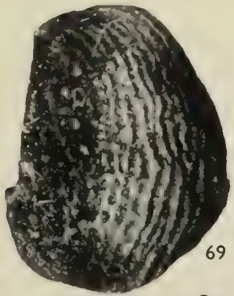
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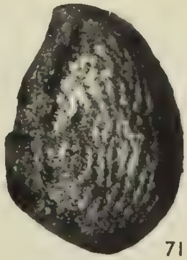
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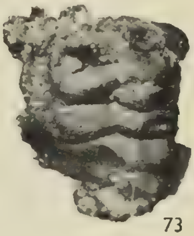
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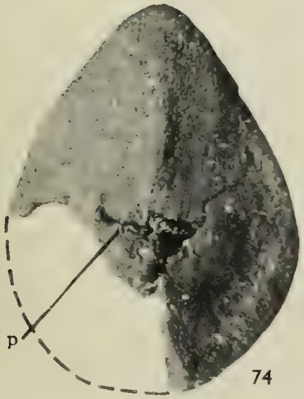

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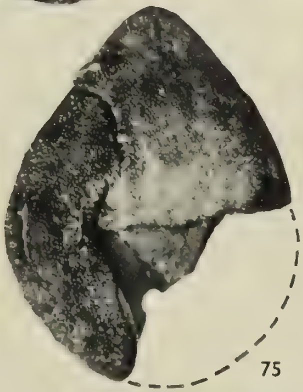
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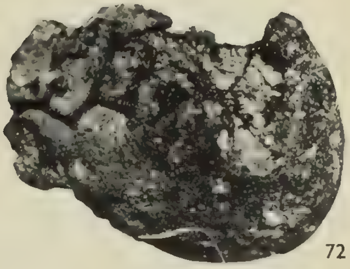
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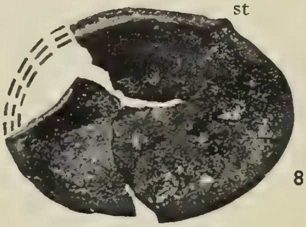

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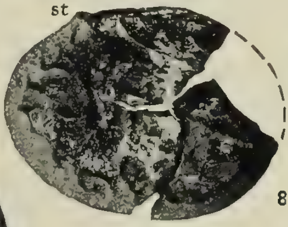

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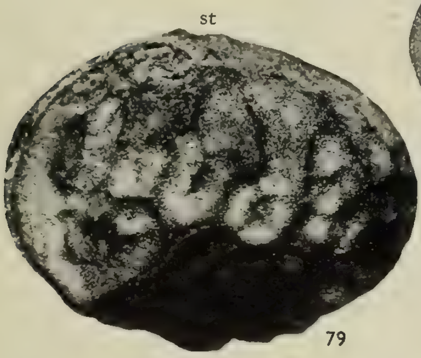

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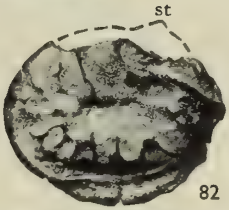

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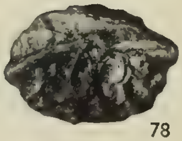
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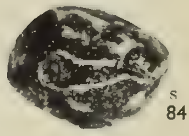

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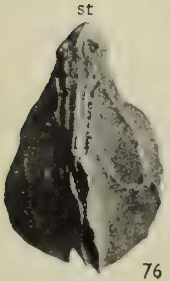

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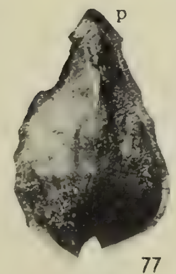

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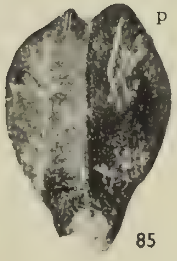

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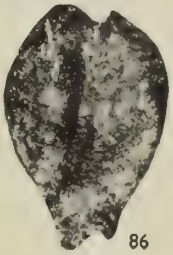
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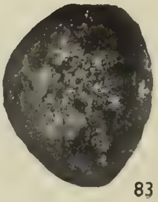
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PLATE 28

Frangula hordwellensis n. sp.

FIG. 87. Seed in figs. 85, 86 fractured longitudinally to show internal surface and (*h*) hilar depression; (*r*) marginal raphe; (*m*) micropyle; (*ch*) chalaza; (*rd*) ridge within hilar depression; (*t*) projecting testa forming rim around this depression. × 15.

Meliosma sp.

FIG. 88. Endocarp. (*a*) Attachment and funicular aperture. × 15·5. (V.42158.)
FIG. 89. Another somewhat broader specimen. × 15·5. (V. 42159.)

Parthenocissus hordwellensis n. sp.

FIG. 90. Seed, dorsal, with chalazal scar. × 6·5. (V.42161.)
FIG. 91. Same, ventral, showing long infolds. × 6·5.
FIG. 92. Another seed, dorsilateral. Chalaza on left. × 6·5. (V.42161.)
FIG. 93. Same, ventrilateral. Raphe ridge on left, facet with long infold seen. × 6·5.
FIG. 94. Poorly preserved seed, dorsilateral. × 6·5. (V.42237.)
FIG. 95. Same, ventral, with infolds. × 6·5.

Figs. 94, 95 from Horizon A3, Barton Beds, Highcliff for comparison.

Tetrastigma lobata Chandler

FIG. 96. Seed, ventral, showing lobing around infolds and raphe ridge. × 6·5. (Decayed.)
FIG. 97. Same, dorsal, showing sunk chalaza and radial lobes and furrows diverging from it. × 6·5.

Actinidia sp.

FIG. 98. Apical rounded end of a seed with pitted surface. × 15. (V.42165.)

Gordonia minima Chandler

FIG. 99. Fruit, lower end (upper part broken) tilted to show receptacle. × 6·5. (V.20070*a*.)

FIG. 100. Another (apex broken) tilted to show interior with broken central columella and bases of three valves below, lower end of two valves at *v*, *v*. × 6·5. (Decayed.)

FIG. 101. Fruit broken transversely showing five locules and septa. Valves triangular in section, columella at centre. × 6·5. (V.20071*b*.)

FIG. 102. Fruit broken above, sectioned longitudinally showing remains of columella and of two valves. × 6·5. (V.20071*a*.)

Eurya becktonensis n. sp.

FIG. 103. Holotype. Seed slightly broken dorsally. (*p*) Coarsely pitted thickening around hilum. × 15. (V.42168.)

Campylospermum hordwellense Chandler

FIG. 104. Fruit, side, with attachment and fruit wall remaining below. × 6·5. (V.20035.)

FIG. 105. Same (as seen from opposite side i.e. in longitudinal section) showing axis and a seed on each side of it. × 6·5.

FIG. 106. Detached seed from another fruit showing beautifully preserved cell structure of testa; (*h*) hilum; (*m*) micropyle. Irregular thickening of coarse cells is well seen in hilar region. × 15. (V.42170.)

FIG. 107. Neotype. Valve of seed showing curved cavity, (*m*) micropyle. Raphe in wall between limbs opening into chalaza at tip of shorter limb. × 15. (V.42169.)

Cleyera ? stigmosa (Ludwig)

FIG. 108. Seed, pitted surface poorly preserved. × 15. (V.42173.)

FIG. 109. Same broken irregularly longitudinally shows condyle between limbs of curved locule. × 15.

FIG. 110. Inner surface of fragment removed by fracture showing same features. × 15.
FIG. 111. Another. × 15. (V.42174.)
FIG. 112. Smaller seed. × 15. (V.42175.)

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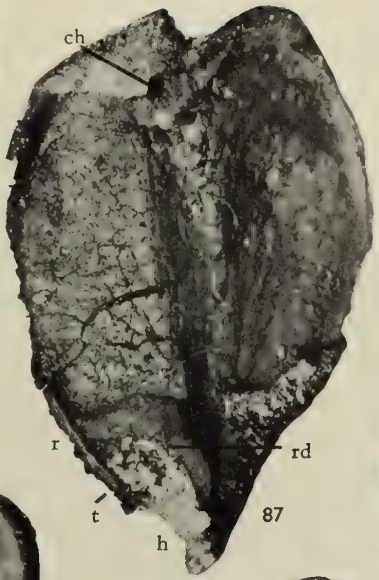

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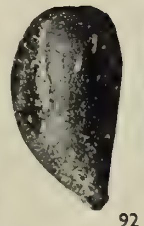

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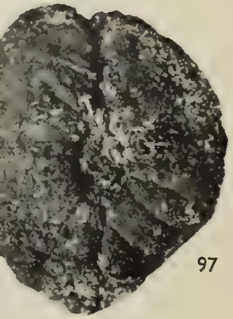

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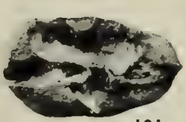

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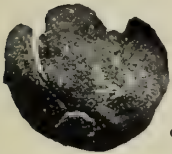

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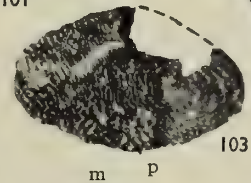

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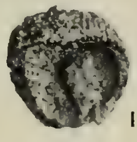

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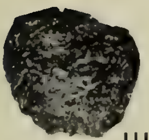

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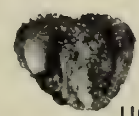

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Anneslea ? *costata* n. sp.

FIGS. 113, 114. Holotype. Seed, opposite surfaces, (*h*) hilum. ×15. (V.42177.)

FIG. 115. Another broken seed dissected to show condyle between curved limbs. ×15. (V.42178.)

Microdiptera parva Chandler

FIG. 116. Seed, dorsal with operculum partly detached but embedded in white matrix. ×15. (V.42182.)

FIG. 117. Same, ventral, showing median longitudinal body, lateral wings breaking away from it. ×15.

Mastixia ? *glandulosa* n. sp.

FIG. 118. Endocarp, dorsal surface with external longitudinal furrow. ×6·5. (V.42188.)

FIG. 119. Holotype. Endocarp, ventral surface. ×6·5. (V.42187.)

FIG. 120. Laterally compressed endocarp with ventral wall removed so as to expose inner surface (*i*) of dorsal infold projecting into locule. ×6·5. (V.42189.)

FIG. 121. Another with part of external wall removed showing solidified resin secretions (light coloured) occupying cavities in middle layer of wall. ×6·5. (V.42190.)

MASTIXIOIDEAE, Genus ?

FIG. 122. Endocarp, apex with two germination valves removed, the third which remains shows an infold at (*i*). ×2 approx. (V.20106*a*.)

FIG. 123. Same, side, one locule exposed by removal of a valve. ×2 approx.

FIG. 124. Upper part of the valve, inner surface showing infold. ×2 approx.

Dunstania glandulosa (Chandler)

FIG. 125. Holotype. Endocarp, broken at base. ×4. (V.20090.)

FIG. 126. Same, sectioned longitudinally showing two locules and resin cavities in walls. ×4.

FIG. 127. Neotype. Endocarp somewhat abraded, shows apex truncated by small depression. ×15. (V.42194.)

FIG. 128. Broader abraded endocarp with resin cavities partly exposed superficially. ×15. (V.42195.)

Cornus quadrilocularis Chandler

FIG. 129. Endocarp, side, apex excavated by small depression. ×6·5. (V.42193.)

FIG. 130. Same, opposite side with a valve partly removed showing locule, the ventral wall of which is broken at apex. ×6·5.

FIG. 131. Another endocarp, side, germination valve removed showing locule and apical depression. ×6·5. (V.20106.)

FIG. 132. Apex of same, three valves have been removed, one remains on left. ×6·5.

FIG. 133. One of valves removed, inner face. ×6·5.

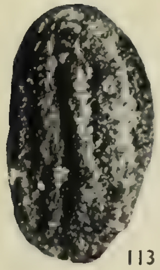
Epacridicarpum headonense Chandler

FIG. 134. Fruit, base. ×15. (V.42197.)

FIG. 135. Same, apex. ×15.

FIG. 136. Valve of another, inner surface showing septum and two locules. ×15. (V.20083.)

FIG. 137. Same, side view, axis to left. ×15.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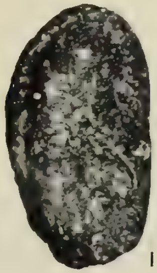
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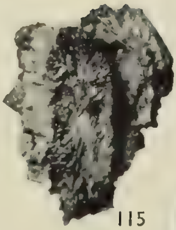
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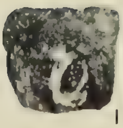
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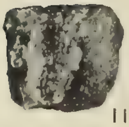
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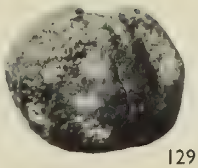
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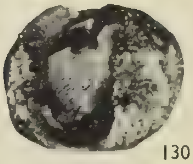
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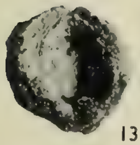
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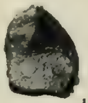
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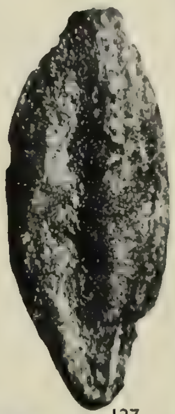
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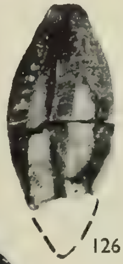
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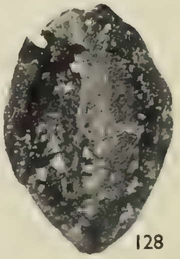
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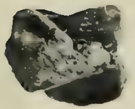
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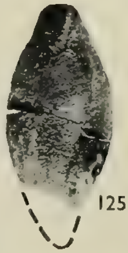
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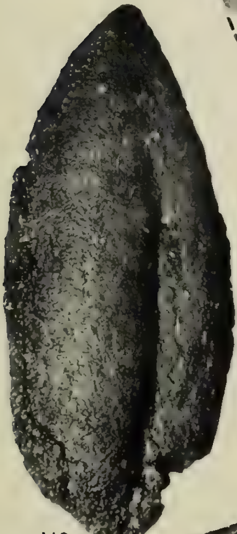
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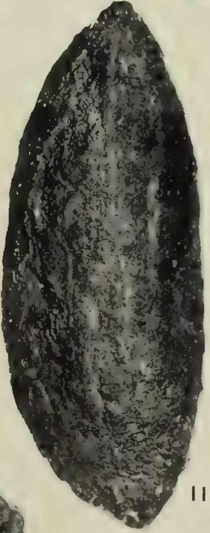
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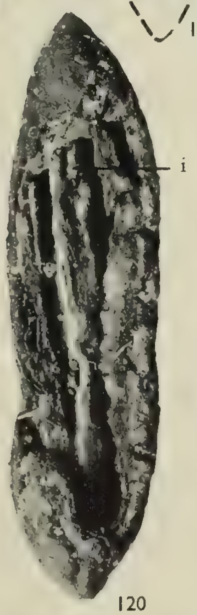
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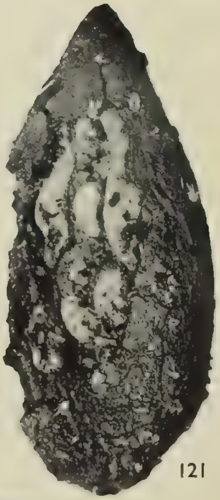
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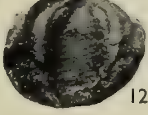
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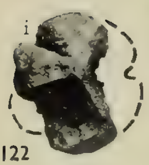

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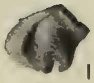
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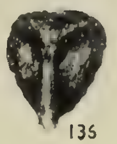
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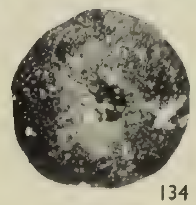
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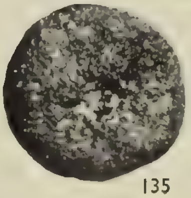
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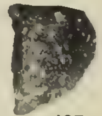
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PLATE 30

Ericaceae, Genus ? sp. 2.

Fig. 138. Fruit, apex showing incipient splitting into valves. ×15. (V.42198.)

Symplocos headonensis Chandler

Fig. 139. Neotype. Endocarp, apex showing depression with four apertures to locules and a central aperture to axial canal. ×6·5. (V. 42202.)

Fig. 140. Endocarp fractured longitudinally showing two locules (filled with white matrix communicating with apical depression). Central canal exposed in upper part of endocarp. At apex behind it is the apical aperture of third locule. ×6·5. (V.42203.)

Olea headonensis n. sp.

Fig. 141. Small endocarp. (*a*) Attachment. ×6·5. (V.42208.)

Fig. 142. Holotype. Valve of endocarp which has split loculicidally. Locule with short oblique funicular canal (*f*). ×6·5. (V.42207.)

Fig. 143. Same, opposite valve, incomplete above, (*f*) funicular canal. ×6·5.

? *Acanthus* sp.

Fig. 144. Seed, side, (*h*) hilum. ×6·5. (V.42213.)

Fig. 145. Same, opposite surface showing characteristic puckering. ×15.

Cucurbitospermum reidii n. sp.

Fig. 146. Holotype. Valve of seed, exterior. ×4. (V.20098.)

Carpolithus apocyniformis n. sp.

Fig. 147. Holotype. Detached valve of capsule imperfect at distal end. Interior with median ridge representing remains of septum. ×15·5. (V.42224.)

Fig. 148. Valve of another capsule, outer surface. ×15·5. (V.42225.)

Carpolithus sp.

Fig. 149. Fruit with three styles. ×6. (V.20110*c*.)

Fig. 150. Fruit with three styles. ×6. (V.20110*b*.)

Fig. 151. Fruit with three styles broken on one side. ×6. (V. 20110*a*.)

Fig. 152. Four-loculed fruit sectioned transversely. ×6. (V.20110*e*.)

Fig. 153. Three-loculed fruit sectioned transversely. ×6 (V.20110*d*.)

Carpolithus sp.

Fig. 154. Six-lobed organ, lobes with slight transverse constrictions. ×6·5. (Decayed.)

Figs. 155, 156. Another, opposite ends. ×6·5. (V.42229.)

Fig. 157. Recent specimen for comparison. Accidental impurity in seed packet from Yokohama Nursery Co. (unidentified). ×6·5.

Carpolithus sp.

Fig. 158. Valve of reniform seed, interior. Hilum between limbs. ×15. (V.42232.)

Carpolithus sp.

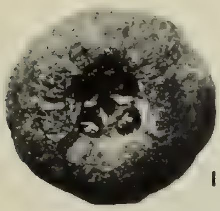
Fig. 159. Imperfect four-loculed endocarp. One valve faces camera but it is broken on left of median line exposing locule beneath it. Another abortive locule on left is not clear in figure; (*l*) is a third locule. The fourth is behind and out of sight. ×6·5. (V.42233.)

Tuber ?

Fig. 160. Organism with rough, scaley, cracking surface. ×6·5. (V.42234.)

Mastixicarpum crassum Chandler

Fig. 161. Endocarp, dorsal, breaking longitudinally along median infold. The transverse fracture showed C-shaped locule. ×2·4. (V.42235.) For comparison with Hordle material. Alleged to come from Barton clay, Barton cliff.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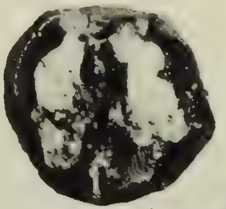
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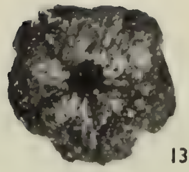
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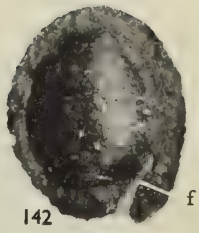

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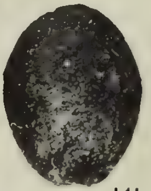

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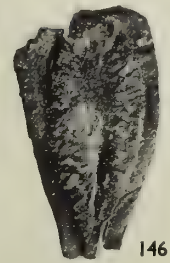
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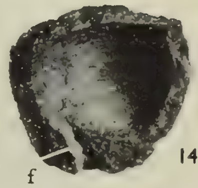

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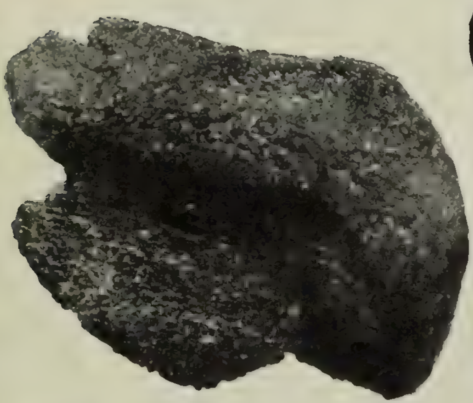
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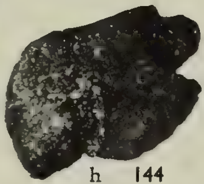

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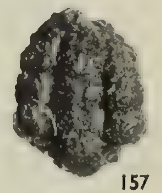
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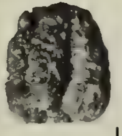
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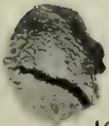
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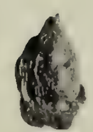
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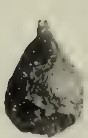
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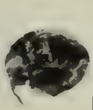
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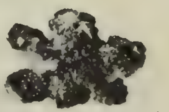
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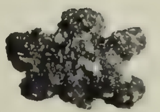
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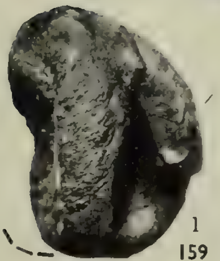

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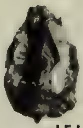
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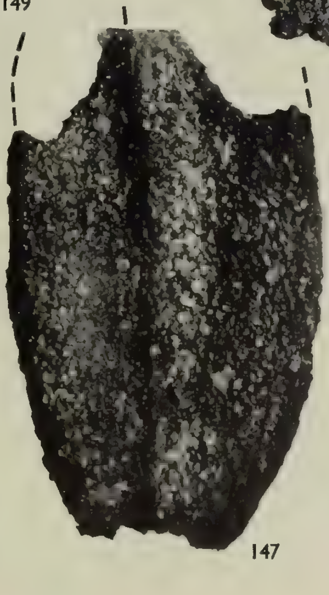
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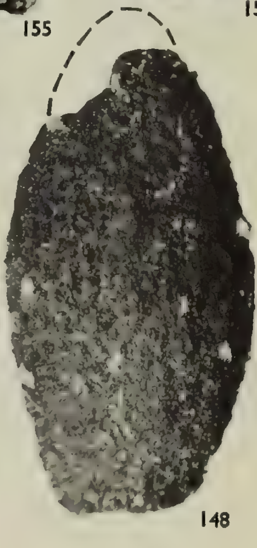
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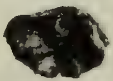
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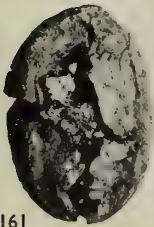
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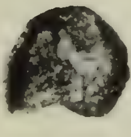
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THE FORM AND STRUCTURE OF *CTENOZAMITES CYCADEA*

THOMAS MAXWELL HARRIS

BRITISH MUSEUM
20 JUL 1961
NATURAL

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THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 5 No. 6
LONDON : 1961

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BY

THOMAS MAXWELL HARRIS, F.R.S.

(Professor of Botany in the University of Reading)

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Pp. 159–173 ; *Plates* 31, 32 ; 2 *Text-figures*

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THE FORM AND STRUCTURE OF *CTENOZAMITES CYCADEA* (BERGER) SCHENK

By T. M. HARRIS

SYNOPSIS

This paper deals with a single magnificent specimen of the Lower Liassic leaf which has been called *Ctenopteris cycadea* (Brongn.). It is nearly complete and shows that the leaf is larger than had been supposed and also proves that the rachis forks. This forking brings *Ctenozamites* close to *Ptilozamites* and possibly also to *Odontopteris*. The specimen has also the merit of being partially petrified and gives some indication about its internal tissues.

INTRODUCTION

THE specimen (V.36330) bears the label " Plant from the Flatstones Nodules, Black Marl, Black Ven, Charmouth, Dorset. Collected by J. F. Jackson, 27-9-58." The rock is from the Flatstones of bed 83 of the Lower Lias succession of Dorset (Lang & Spath, 1926), and contains the well-known ammonites *Asteroceras obtusum* (J. Sowerby) and *Promicroceras planicostata* (J. Sowerby) which fix its age as the Obtusum Subzone, the lowest division of the Obtusum Zone. The specimen was in a large concretion which fell from the cliff and when the boulder was split it was shattered. Most of the pieces were reassembled, including some of the Counterpart, which, together with the Part, was used in the drawing in Text-fig. 1.

The flora of the British Lower Liassic is small and the floras of the Middle and Upper Liassic are even smaller. Land plants occur in its extremely limited freshwater facies (see Kendall, 1949 for West Scotland, Lewarne & Pallot, 1957 and Harris, 1957 for South Wales). In its widespread marine facies, plants, apart from driftwood, seem to be very rare, but a moderate number have been collected over the last century and most of these are magnificent specimens. The flora was described by Seward in 1904 and since then some additional species have been collected and others have been revised.

The flora is as follows (the list may include some from the Rhaetic) :

" *Carpolithes* sp." Seward, 1904.
" ? *Araucarites* sp." Seward, 1904, p. 20.
Cycadolepis sp. (as *Hippurites* Buckman and indeterminable according to Seward, 1904).
Equisetites sp. (as *E. muensteri* Seward, 1904).
Cycadopteris anglica Gothan = *Thinnfeldia rhomboidalis* of Seward, under revision by Townrow & Hancock.
Ctenozamites cycadea (Berger) of this paper = *Ctenopteris cycadea* of Seward.

The previously known specimens are in a soft shale from Lyme Regis.

Cycadites rectangularis Brauns, see Seward, 1904.
Otozamites bechei Brongn. (as *O. obtusus* L. & H. in Seward, 1904 ; see also Harris, 1960).
Cycadeoidea (*Yatesia*) *gracilis*, Seward, 1904. (A *Bucklandia*.)
Cycadeoida pygmaea L. & H. (specimen not seen, see Seward, 1904).
Pagiophyllum peregrinum. See Seward, 1904, Kendall, 1948.
Strobilites elongata L. & H. (specimen not seen ; see Seward, 1904).
Pagiophyllum sewardi Kendall, 1948.

In addition there are in the British Museum a leaf resembling *Stenopteris*, a forked leaf or branch with parallel veined pinnae (or leaves) and some alga-like filaments. In the Geological Survey Museum there are also :

" *Zamites megaphyllos* Phillips " (a large, simple leaf).
" *Cupressinites liasinus* " (possibly distinct from *Pagiophyllum peregrinum*).

Several of these fossils, and also the fossil wood, might yield information beyond what has been published.

The specimens come from numerous quarries and coastal exposures in the SW. of England and by far the richest region is around Lyme Regis, Dorset, which has provided more than half the specimens. Unfortunately the specimens, apart from those collected by Mr. Jackson, are imperfectly localized being merely labelled " Lyme Regis ". Most of them are in a soft black shale, presumably exposed between the tide marks, but the exact locality is lost to memory and the specimens could be from one or more zones. I spent a few days searching at Lyme Regis and merely found a good deal of drift wood, some of it with structure preserved but no leaf or twig. There were no cuticle fragments in the blocks I macerated.

DESCRIPTION

Form. The two pieces fitted together are 55 cm. long, but the apex is lost and so is the base of the rachis. It is possible to estimate the length of the missing top from the taper of the half rachises, which is about 1 mm. in 5 cm. As the width at the top is 7 mm. the missing part might be 35 cm. long, but rather less if the rachis tapered more quickly in the upper and more leafy part and this would seem likely. The petiole increases in width downwards and is about 2 cm. wide at the point where the rock is broken. There is nothing to suggest how much of the original leaf is missing. Thus the leaf, apart from the missing base, may have been 80 or 90 cm. long. The lower pinnae are severely abraded and some must have disappeared altogether, but those between the forks of the rachis which may have been protected are better preserved. The most complete is 11 cm. long, but the pinnae below the fork have distinctly larger pinnules and were perhaps rather longer. It will be noticed that the pinnae of the right fork are alternate and those of the left nearly opposite. The lowest basiscopic pinnules are borne just below the point of attachment of the pinna, that is, on the main rachis, but the plane of cleavage has not followed the specimen perfectly and only a few are seen. These first pinnules arise on the upper surface of the rachis and the later pinnules arise near the top of

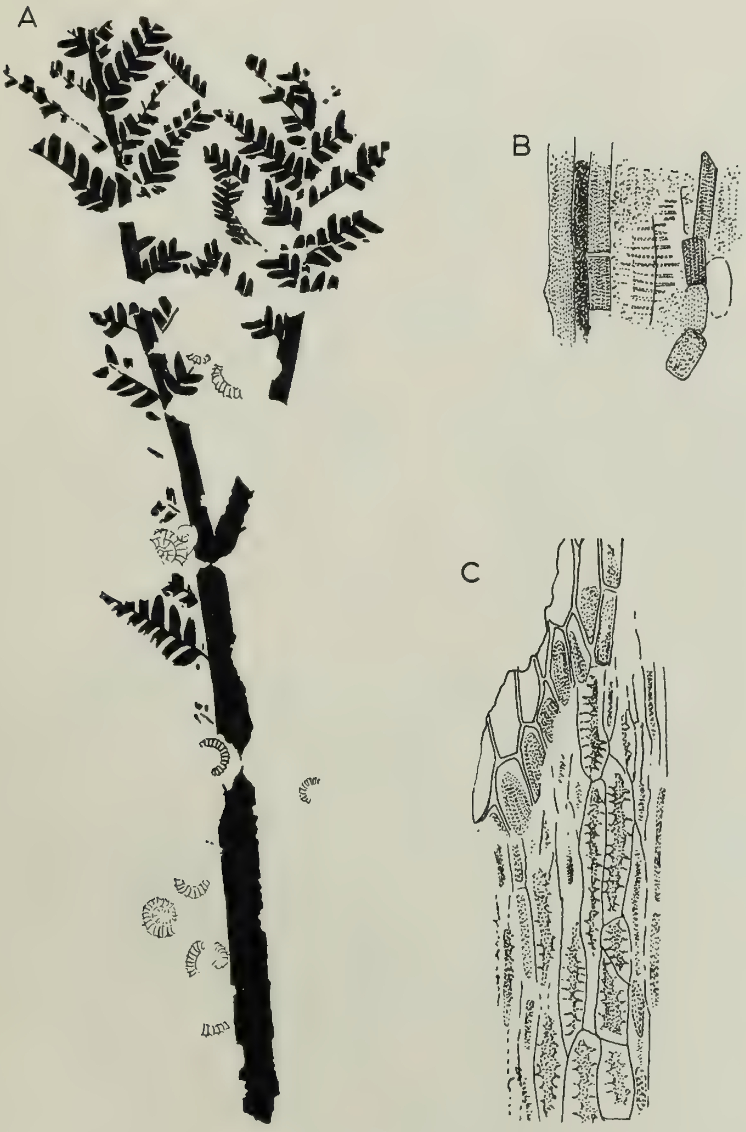

FIG. 1. A, silhouette of the whole specimen, V.36330. There is a gap between the top 4 cm. and the rest. The top is drawn from part and counterpart. Reduced to 1/3 natural size. B, tissues of vascular bundle of rachis in horizontal section, some bundle sheath cells enclose one or two scalariform tracheids, V.36330*a*. × 200. C, surface of rachis in horizontal section, showing from the top downwards : cuticle, epidermal cell contents, stone cells flanked by narrow cells, V.36330*a*. × 200.

the pinna rachis. The pinnules are almost flat but with slightly depressed margins and in none is the margin rolled back. The pinnules have obtuse apices, in none was it mucronate or denticulate. Their veins are clearly seen where the plane of cleavage has passed through them. They diverge slightly and some fork ; maintaining a concentration of about 20 per cm.

Anatomy of lamina. The fossil is preserved in an unusual way, intermediate between a compression and a petrefaction. The lamina is only slightly compressed and when buried in the marine calcareous mud seems to have undergone two changes. The first is that most of the cells became filled with a brown or black bituminous substance (there seems too much of it to represent the original cell contents), and second that the spaces between the cells were filled with calcite. The fossil as exposed is a light brown colour when dry. The lamina cannot be picked off the rock, a hard limestone, but chips can be treated with dilute acid when pieces of the lamina, especially its epidermis are freed. They were studied in three ways:

1. The cuticles were prepared.
2. The internal tissues were teased apart after decalcification.
3. The internal tissues were studied in sections.

The cuticles were rather difficult to prepare because nitric acid attacks the substance of the cuticle almost as rapidly as the mesophyll cells. Good results were obtained as follows :

1. The decalcified epidermis was soaked in moderately strong nitric acid for 10–60 min.

2. It was washed in dilute ammonia.
3. It was left in glycerine on a slide for several hours. This seems to toughen it.
4. The mesophyll cells were carefully teased away from its inner side. Even after this treatment the cell contents remain and the preparation is of the epidermis rather than purely of the cuticle.

The isolation of internal tissues by teasing was only moderately successful. The palisade mesophyll cells are very conspicuous as little dark cylinders representing their contents ; their walls are not seen in teased preparations.

The upper cuticle is thick and shows the outlines of polygonal epidermal cells. These cells are almost uniform, the veins being scarcely distinguishable. The outlines of the cells are marked by broad but by no means prominent ridges. The sides of the cells are straight but interrupted by a few pits. The surface walls are flat and the surface may be finely granular or the granules may be elongated and this appearance seems to pass gradually into a system of fine parallel striations orientated longitudinally. Only one trichome base was seen on the upper side (Text-fig. 2F) ; it is like those along the veins on the lower side and consists of a small rounded cell on top of the ordinary epidermal cells.

The lower cuticle is also thick. The cells are like those of the upper side, but smaller and the veins are clearly shown by about five rows of elongated rectangular cells and no stomata ; the wide intervenal areas have irregular or isodiametric cells and numerous scattered stomata. The guard cells are mostly longitudinally orientated or more or less oblique, but seldom transverse. They are at the bottom

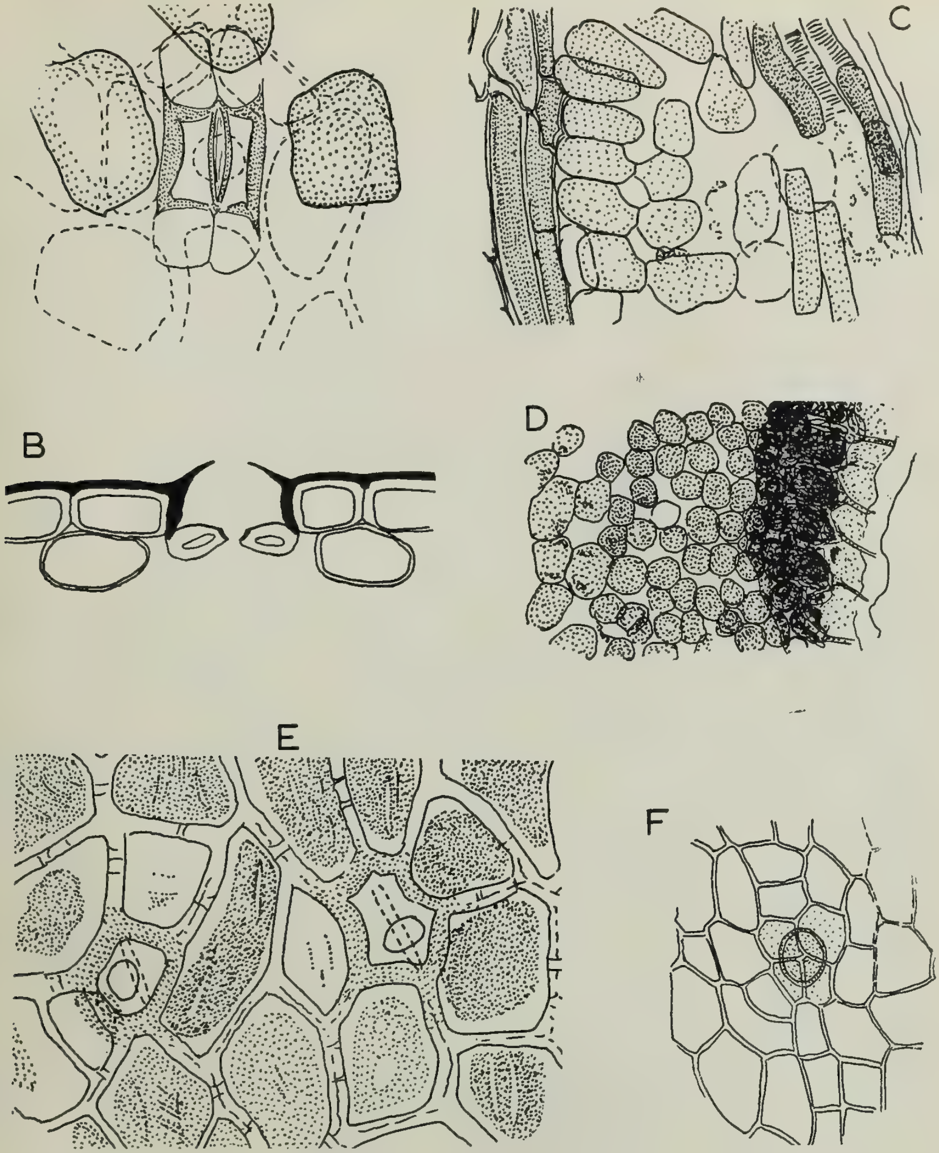

FIG. 2. *Tissues of lamina*

A, a stoma seen from within. A few mesophyll cells remain ; the epidermis at a deeper level of focus is shown by broken lines, V.36330*b*. × 800. B, imaginary T.S. through A, the vertical distances being determined by focusing. Cuticle in black, other walls outlined, × 800. C, horizontal section through middle of mesophyll showing a vein with sheath and tracheids (right) and the sheath along (left), V.36330*c*. × 200. D, horizontal section through upper surface of lamina showing from right to left, cuticle, epidermal cell walls, epidermal cell contents, outer layer of palisade, deeper layer of palisade mesophyll, V.36330*d*. × 200. E, lower cuticle from outside. The content is still present in most epidermal cells. Faint surface striations are shown by dotted lines and the guard cell aperture at a deeper focus by a pair of broken lines, V.36330*b*. × 800. F, upper cuticle showing a complex trichome base, V.36330*e*. × 200.

of a polygonal or rectangular pit with a thickly cutinized wall formed by an irregular ring of about six subsidiary cells. The mouth of the pit is covered by a strongly raised dome (almost a hemisphere) of thin cuticle. The top of this dome is pierced by a hole which may be round or oval and is often more or less transversely elongated. Encircling cells may occur but are inconstant.

The guard cell surface is thinly cutinized but there is a slightly thickened band by the aperture. The aperture itself is arched, the middle part being more deeply sunken than the ends. The outline of the poles of the guard cells can just be traced, but nothing remains of any lignine thickenings originally present in the guard cells.

The epidermis is scarcely compressed and it was possible to recognize differences of level of the stomata by focusing. The top of the dome is about 8 μ above the general surface of the cuticle and the middle part of the stomatal aperture is about 8 μ below this surface.

Trichome bases are frequent on the veins and consist of one or occasionally two small oval cells on top of the ordinary cells. Sometimes a ring is visible on the surface of one of these cells but more often the whole cell surface would seem to have been covered by the trichome. No hypodermal cells occur, but fibres along the veins come close to the upper epidermis.

The mesophyll was studied successfully both by maceration and horizontal sections. The palisade mesophyll is well developed and consists of at least two, probably more, layers of closely packed cylindrical cells 20 μ wide and 50 μ long. In the middle region of the lamina, at the sides of the veins, the mesophyll cells are oval and orientated transversely. Their walls appear to be thin. In the lower part of the leaf the mesophyll cells are of irregular shapes, but next the lower epidermis they are oval again. There is a gap above each stoma and the mesophyll cells here tend to be rather elongated, about five forming a ring. The veins were seen in sections. They have a sheath of elongated cells with massive dark contents. These cells appear to have transverse ends, but it is difficult to distinguish between a transverse break and a true end. The walls as far as they were seen are only moderately thick and not obviously pitted. This sheath is in contact with the spongy mesophyll and encloses various narrow elongated cells, which have little or no bituminous filling but are merely preserved as poorly seen walls. Most of these elongated cells are narrow and show no obvious features, they presumably are fibres and perhaps sieve tubes. In addition a few small tracheids were seen. They have scalariform thickening.

The leaf contains no resin cavities in the mesophyll. There is no sign of any secretory duct in the veins, but unless such a duct had obvious contents it might be hard to recognize in horizontal section.

Anatomy of rachis. The rachises are preserved in the same way as the lamina, but underwent far more compression before they were calcified. Thus the main rachis or petiole which is 2 cm. wide is barely 1 mm. thick in the fossil. Most of its substance has been lost, but a few small chips were obtained when pieces covered by the matrix were exposed. As with the lamina, the plane of cleavage passes through the rachis substance rather than outside it, so each fragment has one epidermis and more or less of the internal tissues. The broken surface showed elongated cells but nothing else clearly.

Good pieces of cutinized epidermis together with isolated cells from the interior were obtained by soaking chips in dilute acid. These represent the various thick-walled tissues seen in the sections, apart from the tracheids which did not survive this treatment. Sections were again cut in a nearly horizontal plane but efforts to obtain more transverse ones gave no useful result.

The epidermis is probably more thickly cutinized than that of the lamina and it was easy to obtain a good preparation, though the dark contents of the epidermal cells usually remains. The cells are elongated and have straight, conspicuous walls and the surface is longitudinally striated. No trichomes were seen but stomata are rather frequent and well developed. The subsidiary cell group is elongated, the guard cells longitudinal and the pore in the dome is rather large and also longitudinally orientated. A well developed sclerotic layer occurs underneath the epidermis. This layer has at least three sorts of cells. The most conspicuous are thick-walled cells looking like elongated stone cells and with conspicuously pitted walls. Then there are strands of narrow fibre-like cells without much contents. Finally there are short thin-walled cells full of black contents which are regarded as assimilatory parenchyma. Some of these are just under a stoma where they are arranged in a ring to form a substomatal air cavity. In the cells like stone cells the dark content is slightly contracted and forms spikes which are evidently the filling of large pits. The cell wall is not very clearly seen but the pits show that it was thick. The ends of these cells may be more or less transverse, or they may be obtusely pointed. This sclerotic layer is by no means thick, in the slightly oblique section it appears about five times as broad as the epidermis so that it can be inferred that it is about five times as thick.

The tissue inside the sclerotic layer which must have formed most of the massive petiole shows several kinds of cells, but most of it is disorganized to a brown humus-like substance. It may well be that this substance was originally parenchyma but the outlines of its cells are not clearly seen. This contrasts with the lamina where the mesophyll cells were filled with dark bituminous matter and very clearly seen.

Most of the cells clearly preserved in the interior of the petiole are elongated ones with dark contents and just like those forming the bundle sheath in the lamina. In the horizontal section these cells form numerous longitudinal files and while some of them probably form bundle sheaths, they are so numerous that most are probably scattered through the tissues. Numerous small vascular bundles were recognized by the presence of scalariform tracheids (Text-fig. 2) but as in the lamina these tracheids were poorly preserved. No massive strands of tracheids occur. In a few bundles there are possibly tracheids transitional between scalariform and multiseriate pitted, that is to say they seem to have thick walls marked with longitudinal rows of small oval pits. The appearance was, however, obscure and it is possible that the cells concerned are of different nature. The bundles include other elongated cells but nothing could be learnt about the arrangement of the cells in these bundles.

DISCUSSION

1. *Determination.* This specimen, apart from being more complete than usual, agrees in every respect with typical leaves of *Ctenozamites cycadea* and with no other species. *C. cycadea* was already known from this locality and if only a small part from the top had been collected it would have been an ordinary specimen. Indeed if no more than one or two pinnules showing their venation had been available, as in Berger's holotype, it could still have been determined with confidence. The most similar fossils are other species of *Ctenozamites*, particularly the Oolitic *C. leckenbyi* where, however, the pinnules are usually longer and acuminate and *Ptilozamites nilssoni* of the Rhaetic (see Harris, 1932), where the leaf is simply pinnate but small fragments look similar.

The cuticle of the present specimen looks just like that of a French specimen figured by Mme. Corsin (1950). It also agrees with the upper cuticles (which alone could be prepared) of the English Liassic leaf, Brit. Mus. (N.H.) no. 40, 674, and with the specimen figured by Saporta (1873, pl. 40, fig. 2) of which Dr. Archangelsky showed me a preparation. The cuticle thus fully confirms the identification.

To judge from its pinnules the present specimen was a leaf of average size. Fragments with smaller pinnules have been figured as for example by Schenk (1887) and these might belong to smaller leaves but there are also fragments with distinctly larger pinnules, as for example, Brit. Mus. (N.H.) no. 40, 674, figured by Seward (1904, pl. 3, fig. 1). The detached pinnule which Mme. Corsin (1950) determined as *Ctenopteris* cf. *sarrani* may be an unusually large form of *Ctenozamites cycadea* (with which it is associated) and if so may represent a leaf twice as large as the present specimen.

2. *Habitat and age.* The present specimen and the two others known from England were found near Lyme Regis, Dorset, in marine Lower Lias. The limestone there is well provided with ammonites, but it also contains very occasional leaves and pieces of wood of land plants. The French specimens figured by Saporta (1873) seem to have a similar origin and so apparently do the German ones of Germar (1847) and Salfeld (1912). This occurrence in marine rocks may be significant even though it also occurs in rocks of fresh water origin (Corsin, 1950). It would be interesting to know more about the provenance of the numerous other specimens described.

If this species does prove exceptionally common in marine rocks, it would suggest that the plant grew near the sea, perhaps near the strand of a tidal river, where it would have a special chance of being preserved at the sea bottom. The same may be true of *Otozamites bechei* (*O. obtusus*).

The present specimen is well dated, being in a matrix full of ammonites, and many others are in rocks zoned by ammonites as Lower Liassic age, as in several parts of Germany (see Salfeld, 1907, 1909). It also occurs in localities regarded as Rhaetic, but some of these belong to the " Grenzschichten " which were formerly regarded as Rhaetic, but shown by Gothan (1914) to be Lower Liassic.

The age of others may be unsettled, but I am not aware of any specimen of *C. cycadea* which occurs in beds with the Rhaetic *Pteria contorta*. The question is worth investigation because this should be a valuable zone fossil.

Specimens agreeing with *C. cycadea* have been found in the Lower Oolite of Roseberry Topping, Yorkshire. If these are correctly determined the species would extend through the Lias.

3. *Nomenclature.*

Select list of references to *Ctenozamites cycadea* :

1832 *Odontopteris cycadea* Berger, p. 23, pl. 3, figs. 2, 3.
1836 *Filicites cycadea* (Berger) Brongniart, p. 387, pl. 129, figs. 2, 3.
1873 *Ctenopteris cycadea* (Brongniart) Saporta, p. 355, pl. 40, figs. 2–5, pl. 41, fig. 1, 2.
1882 *Ctenopteris cycadea* (Brongn.) : Staub, p. 249 and plate.
1886 *Ctenozamites bergeri* (Goeppert) Nathorst, p. 122 (Name).
1887 *Ctenozamites cycadea* (Brongn.) Schenk, p. 5, pl. 3, fig. 11–16a, pl. 4, fig. 18 ; pl. 6, fig. 30 ; pl. 7, fig. 36 ; pl. 8, fig. 43 ; pl. 9, fig. 54. (Includes a forked specimen.)
1904 *Ctenopteris cycadea* (Brongn.) : Seward, p. 36, pl. 3 ; fig. 1, 1*a* ; probably text-fig. 2.
1950 *Ctenopteris cycadea* (Brongn.) : Corsin, p. 258, pl. 11, fig. 3 ; pl. 12, figs. 6–11, text-figs. 6, 8. (Perhaps large pinnules and cuticles described as *C.* cf. *sarrani* should also be included in *C. cycadea.*)

The name used for this leaf by most authors is *Ctenopteris cycadea* (Brongn.), but both generic name and authority are wrong. The first specimens described, and fortunately reasonably well figured, were those called *Odontopteris cycadea* by Berger (1832) from the Rhaetic (or Lower Lias) of SW. Germany. Some have suggested that " *Filicites agardhiana* " of Brongniart (1824) belonged to it but both Nathorst (1909) and Antevs (1919) who examined the Swedish specimen agree that it does not, but very probably is a bad specimen of *Dictyophyllum nilssoni*. Possibly the reason why the species has been attributed to Brongniart rather than to Berger is that the first part of Brongniart's Histoire appeared in 1828, and the fact that Liv. 10 with *Filicites cycadea* only appeared after Berger's work is overlooked. Thus Salfeld (1909) gives the *F. cycadea* reference as 1828, but this is a mistake. Brongniart cites Berger's reference and makes it quite plain that he took the specific name from Berger. It is not likely that Goeppert added to this confusion by changing the specific name to *Bergeri* because everyone seems to have known that it was a later substitution. The name *Bergeri* has been dropped for many years.

The generic name *Ctenopteris* was first used for this fossil by Saporta in 1873. He took the name from a manuscript of Brongniart and published it as Brongniart's genus, though Saporta would seem to be the responsible author. The question who is the author of *Ctenopteris* is, however, immaterial because the name is not valid, being an homonym, *Ctenopteris* having been used by Blume in 1828 as a genus of Recent ferns (allied to *Grammitis*). I am indebted to Dr. R. E. Holttum for pointing this out.

Nathorst (1886) instituted the new name *Ctenozamites* to replace *Ctenopteris*, not on the grounds that it was a homonym, of which he was unaware, but because he considered it unsuitable. He was convinced that the plant was no fern but some kind of Cycad and allied to *Ptilozamites*. Few authors accepted this but continued to use *Ctenopteris* on the grounds of priority, or because they thought it a fern. However, Schenk (1887) used the combination *Ctenozamites cycadea*. Nathorst gave no diagnosis nor adequate description but he made it clear that the name was to be used for *Odontopteris bergeri* (which he recognized as the same as *Ctenopteris cycadea*) and for *C. leckenbyi* from the Oolite of Yorkshire.

4. *Morphology*. The main new fact contributed here is that the rachis forks. Although the specimen has been damaged by the cliff fall or when collected, the continuity of the two branches is fortunately still visible.

This forking might have been recognized long ago because one of the specimens figured by Schenk (1887, pl. 3, fig. 13) shows forking, though at a point much nearer the leaf apex. Possibly forking is variable, or, as in *Ptilozamites nilssoni*, some leaves may fork twice.

5. *Anatomy*. The new facts here contributed about the anatomy of the lamina and rachis do give some help for comparison, but not much. Their main value lies perhaps in that they prove that plants with structure preserved are to be found in limestone nodules near Lyme Regis, and the information we have should be sufficient to identify another and less compressed petiole when one is found. Search should be made.

Apart from its stoma the lamina is unspecialized. It lacks, for example, the strongly developed transfusion parenchyma of many Recent Cycadales and also their hypodermis, but these facts are not ones to which comparative anatomists give weight. The stoma is more useful ; it is haplocheilic as in most Gymnosperms and this distinguishes it sharply from all Bennettitales. The general arrangement of the subsidiary cells and the arched shape of the guard cells agrees closely with the Cycadales but less closely with Conifers or *Ginkgo* or such few Pteridosperms as we know. The dome of cuticle over the stomatal pit is a peculiar feature shared by a few fossils, *Ptilozamites* spp. and certain species of *Pseudoctenis* and not seen in any Recent Cycad though Cycads do not differ fundamentally. The rachis, as far as it is known, may be very like that of a Cycad. The subepidermal sclerotic tissue may be a similar mixture of thick-walled fibres and assimilatory cells but the thick-walled fibres of Cycads are at least in several genera, longer and less freely pitted. In having small vascular bundles with scalariform tracheids it agrees with Cycads. These features are by no means exclusive of Cycadales, for they occur, for example, in the petiole of *Medullosa*.

6. *Systematic position*. The four best known species of *Ctenozamites* make a compact group and it is reasonable to regard them as forming a natural genus and to discuss them together.

These four are :

Ctenozamites cycadea (Berger) Schenk.
Ctenozamites leckenbyi (Leckenby) Nathorst (see Harris, 1943).
Ctenozamites sarrani (Zeiller) nov. comb. for *Ctenopteris sarrani* Zeiller, 1903 : 53, pls. 6–8.
Ctenozamites wolfiana (Gothan) nov. comb. for *Ctenopteris wolfiana* Gothan, 1914 : 142, pl. 26, figs. 2, 2*a*, 5, pl. 37, figs. 5, 6. A dozen other species have been

described but are either poorly known or probably belong to other genera and they are not considered here.

C. cycadea and its allies were at first regarded as species of *Odontopteris* or allied to that genus and some kind of fern, and later by Nathorst as Cycads allied to *Ptilozamites*. It is now generally regarded as a Gymnosperm and by different authors placed more or less close to the Cycadales. Nathorst was chiefly impressed by the leathery texture of *C. cycadea* and the close resemblance between a pinna fragment of *C. cycadea* and a piece of the rachis of *Ptilozamites nilssoni*. To these we can add the very close resemblance of their cuticles, particularly their stomata, and the fact that the main rachis in both forks. The only important difference is that the leaf is once pinnate in *Ptilozamites* but bipinnate in *Ctenozamites*. We have no evidence to show whether the rachis forks in the other three species of *Ctenozamites*, but in *Ptilozamites* we are almost certain that it is simple in some species. While the difference between a simply pinnate and a bipinnate leaf is so obvious that it makes a basis for generic grouping of fossil leaves that is too useful to neglect, one may suspect that the plants could all have belonged to one natural genus.

We know nothing about the reproductive organs or other parts of the plant bearing *Ctenozamites* leaves, but we have probably the pollen producing organs of *Ptilozamites nilssoni*. These were described by Harris (1932) under the incorrect determination " *Hydropteridangium* " or *Hydropterangium marsilioides* Halle and renamed *Harrisia marsilioides* by Lundblad (1950) and then as *Harrisothecium marsilioides* by Lundblad (1961). It was attributed to *P. nilssoni* on the evidence of association and agreement in stomatal structure. This fructification is like a loosely organized cone, but its morphology is obscure. The main axis branches in all planes, the branches themselves branch and end in 2-valved capsules. Each valve contains a row of elongated microsporangia with pollen grains, each with two nearly opposite air sacs. If we may accept that *Harrisothecium* belongs to *Ptilozamites* its value in classification is negative in that it provides evidence against including the plant in the Cycadales and indeed in any other established group. The capsules look like those of *Williamsonia* or *Cycadeoidea* but they differ completely in pollen, and stomata, and in the mode of branching.

Ctenozamites (" *Ctenopteris* ") has been classified as possibly Cycadalean, possibly a Pteridosperm, a Cycadophyte or just a Gymnosperm *incertae sedis*. There is very little reason for preferring one to another, except that if the fructification is like *Harrisothecium* the Cycadales would be excluded and so would the Pteridosperms unless we extend the meaning of that extensive class still further. Whether it is a " Cycadophyte " is a matter of definition. The term is for many no more than a convenient abbreviation for the phrase " A Mesozoic Gymnosperm with a pinnately constructed leaf and *any* sort of reproductive organ ". It includes Cycadales and Bennettitales with totally different reproductive organs and stomata. If " Cycadophyte " is used in this way, *Ctenozamites* would be placed there readily enough. For other authors " Cycadophyte " is supposed to be some kind of large family of plants with a relationship that is real even if rather obscure. This is near to its original meaning and if such meaning is held, *Ctenozamites* should be left *incertae sedis*, and indeed the term Cycadophyte should be abandoned.

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PLATE 31

Ctenozamites cycadea (Berger)

Upper part of the specimen. Counterpart of what is shown in Text-fig. 1, A. × 1. V.36330.

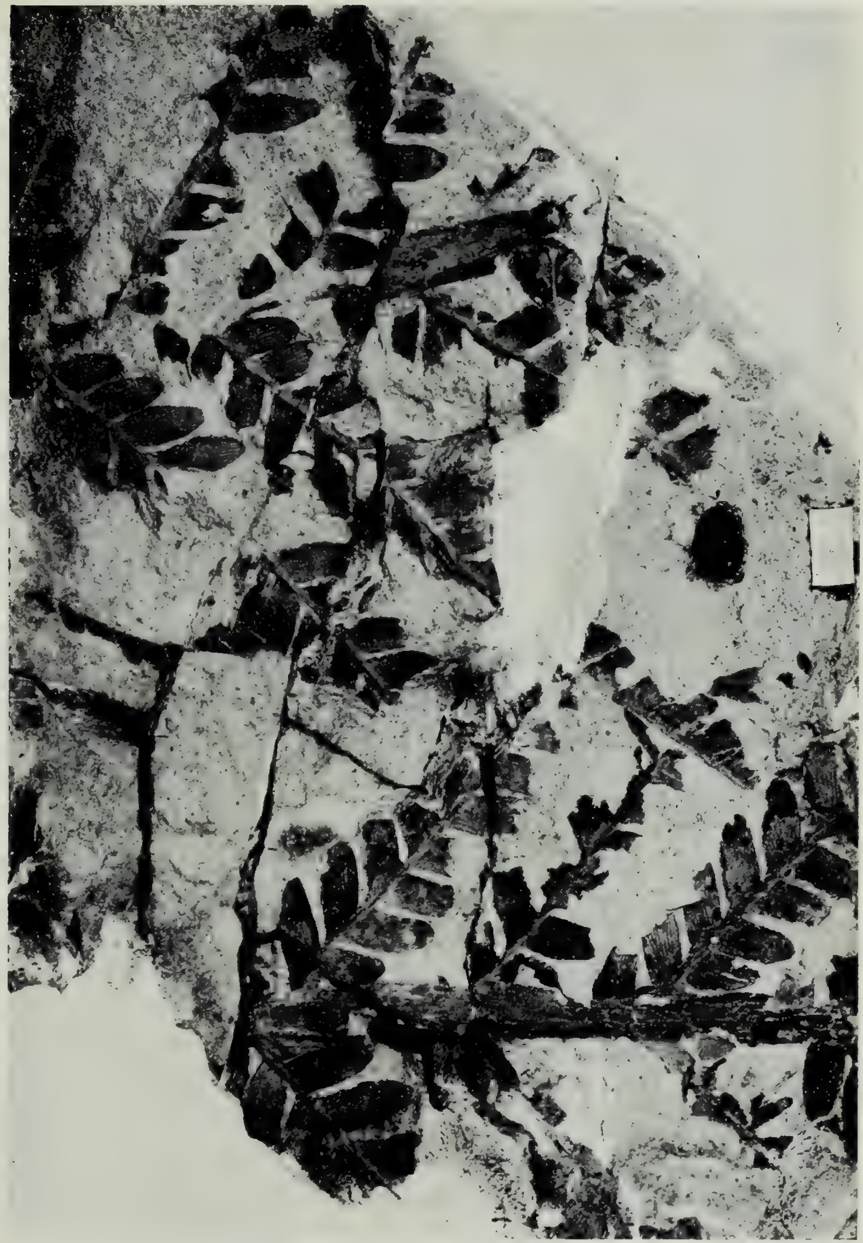


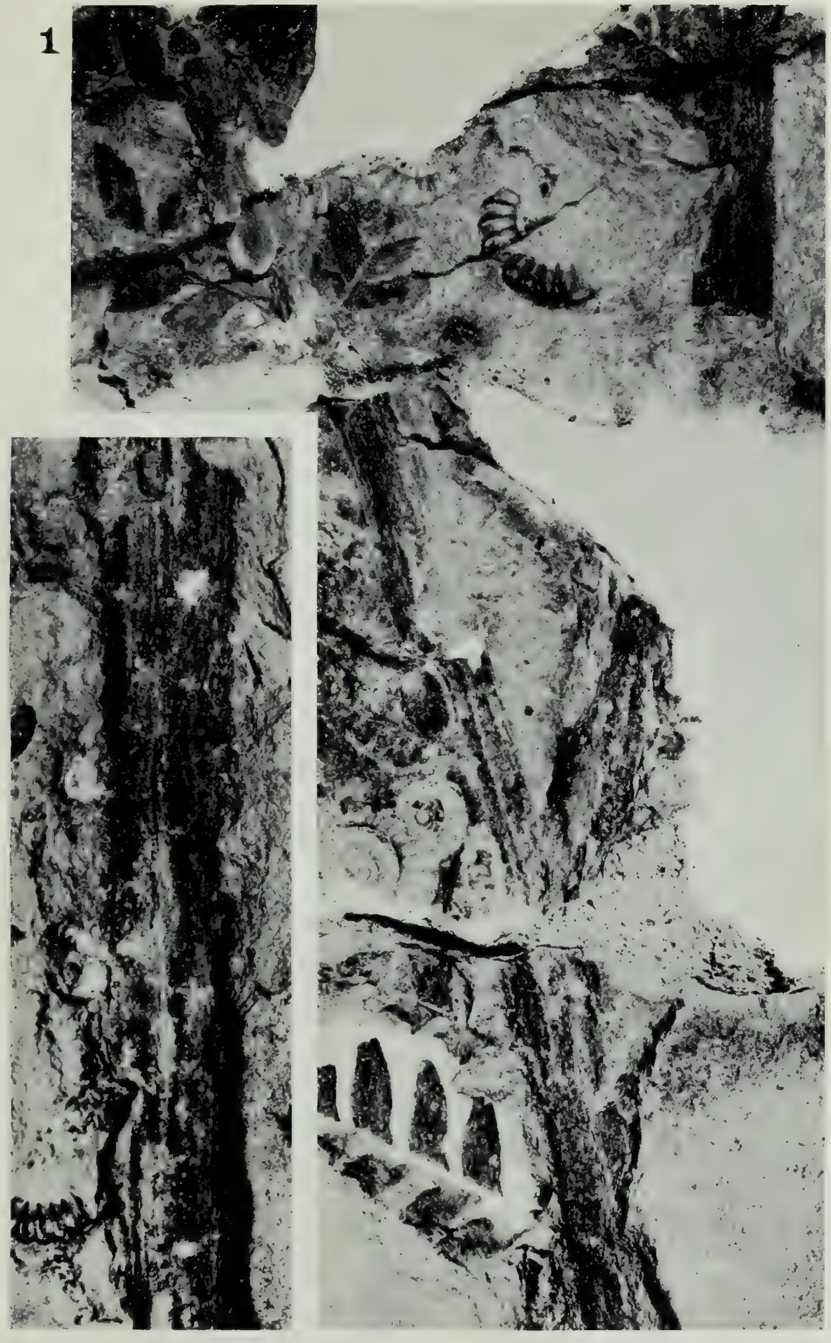
PLATE 32

Ctenozamites cycadea (Berger)

FIG. 1. The rachis dichotomy. × 1.

FIG. 2. The lower part of the rachis showing stumps of two pinnae. × 1.

1



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THE OLD RED SANDSTONE OF BROWN CLEE HILL AND THE ADJACENT AREA

I. STRATIGRAPHY

H. W. BALL AND D. L. DINELEY

II. PALAEONTOLOGY

E. I. WHITE

BRITISH MUSEUM
12 OCT 1961
NATURAL HISTORY

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GEOLOGY Vol. 5 No. 7
LONDON : 1961

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BY

HAROLD WILLIAM BALL

AND

DAVID LAWRENCE DINELEY

Pp. 175–242 ; 2 *Text-figures,* 1 *table,* 1 *map*

II. PALAEONTOLOGY

BY

ERROL IVOR WHITE, F.R.S.

Pp. 243–310 ; *Pls.* 33–48 ; 61 *Text-figures*

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THE OLD RED SANDSTONE OF BROWN CLEE HILL AND THE ADJACENT AREA

This paper is dedicated to the late William Wickham King

PART I. STRATIGRAPHY

By HAROLD WILLIAM BALL & DAVID LAWRENCE DINELEY

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SYNOPSIS

The stratigraphical and faunal succession of the Old Red Sandstone, which forms the greater part of the area about Brown Clee Hill, Shropshire, is described. The Lower Old Red Sandstone forms a conformable sequence which is subdivided into the Downton, Ditton and Clee Series. The base of the Downton Series (Downtonian) is demarcated by the Ludlow Bone Bed, and the Series shows a gradation from predominantly buff and grey sediments (Grey Downton Formation) to purple and red beds (Red Downton Formation) which include local developments of sandstones near the top. The upper part of the Downton Series falls within the zone of *Traquairaspis symondsi*. The Ditton Series (Dittonian) commences with the main " *Psammosteus* " Limestone ; it is subdivided into a lower group composed largely of red and purple marls with sandstones and cornstones, broadly equating with the zones of *Pteraspis* (*Simopteraspis*) *leathensis* and *Pteraspis* (*Belgicaspis*) *crouchi*, and an upper group in which the marls are largely replaced by silts, with an increase in the proportion of sandstones and cornstones, and a change to predominantly red-brown, brown-buff and grey-green coloration. The upper group corresponds to the zone of *Pteraspis* (*Cymripteraspis*) *leachi*. The Clee Series (Breconian) consists largely of unfossiliferous grey, buff, brown and purple sandstones and silts, the base of the Series being formed by the lower Abdon Limestone. This sequence is unconformably overlain by the Upper Old Red Sandstone comprising the Farlow Sandstone Series (Farlovian), which is subdivided into a lower (Yellow) and an upper (Grey) Formation. A further unconformity occurs between the Farlow Sandstone Series and the basal conglomerate of the Carboniferous. An account is also given of the structure and geological history of the area.

The fauna is discussed and five new genera, one new subgenus and fifteen new species are described and figured.

I. INTRODUCTION

(a) *Geographical Setting*

DOMINATING the area to be described is Brown Clee Hill which has an " hour-glass " shape and is elongated in a N.–S. direction. The hill is largely composed of beds of Breconian age folded into a syncline, the axis of which extends NNE.–SSW. thus diverging slightly from the hill's topographical axis. A thin series of Coal Measures unconformably overlies the Breconian and is in turn capped by the remnants of dolerite sheets[1] at Abdon Burf and Clee Burf, the northern and southern eminences respectively, the former at 1,790 ft. O. D. being the highest point in the Midlands.

Brown Clee Hill is connected by relatively high saddles with Titterstone Clee Hill to the south and Weston Hill to the south-west, whilst west and north extends the high level platform of Ditton Priors. This platform is formed by the Ditton Series and bounded by the prominent escarpment of the sandstones associated with the " *Psammosteus* " Limestones. Below the escarpment to the west lies Corvedale, incised into the less resistant strata of the Downton Series and drained to the south-west by the River Corve ; to the south-east a smaller complementary valley has been cut by the Ledwyche Brook.

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[1] A contact between the top of the dolerite and the base of the overlying carbonaceous shales, exposed in the old quarry at Clee Burf, showed the shales to be baked to a depth of 2 in., supporting Marshall's (1942) interpretation of the intrusive form of the Clee dolerites as opposed to Pocock's (1931) extrusion hypothesis.

To the east, between Brown Clee and the Coal Measures of the Wyre Forest, a broad outcrop of Ditton Series gives rise to more undulating topography, the cornstone and sandstone horizons characteristic of this Series forming numerous minor ridges and escarpments. The southern margin of the area is demarcated by the scarp slope of the Cornbrook Sandstone which forms the north flank of Titterstone Clee Hill, and by the ridge of the Farlow Sandstone Series and the overlying Carboniferous Limestone extending eastwards from Farlow. The drainage of the area to the east of Brown Clee Hill centres upon the River Rea which flows to the south-south-east, breaching the Farlow ridge at Prescott and ultimately joining the River Teme, as does its western neighbour the Corve.

(b) *Historical Review*

Despite the relatively numerous references to the geology of the area, most of our knowledge is based upon the researches of two authors. The first of these was Murchison, who gave the fullest account in his epic *Silurian System* (1839), subsequent versions of which appeared in the several editions of his *Siluria*. It was almost a century later that the other major contributions appeared by W. Wickham King (1925, 1934) who established the first detailed succession based on lithological characteristics.

More recently, White (1950*a* ; White & Toombs, 1948) has suggested a modification of this succession to conform with the results yielded by his valuable researches into the ostracoderm faunas of the Old Red Sandstone of the Welsh Borderland and South Wales. Other contributions to the vertebrate palaeontology of the area have been those of Egerton (1862), Stensiö (1932, 1948), A. S. Woodward (1934) and Wills (1935).

The area was first systematically mapped by Robert and Romley Wright during the early part of the last century, as noted by Murchison (1839 : 112) who also appended a map and sections to the *Silurian System*. These were followed by the Geological Survey during the period 1850–55, the results being published in the Old Series 1-in. scale maps, sheets 55 NW. and NE., and 61 SW. and SE. The eastern extremity of the area is included on the New Series 1-in. scale map, sheet 167, and some interesting conclusions regarding the subdivision of the Lower Old Red Sandstone are included in the Memoir on the sheet (Whitehead & Pocock, 1947).

The present account, based on mapping on a scale of 6 in. to a mile and in some instances 25 in. to a mile, originated as two independent pieces of research, one author working upwards from the Downtonian, the other working downward from the Farlovian, both meeting in the common ground of the Dittonian. Thus one of us (D. L. D.) is entirely responsible for observations on the succession ranging upwards from the base of the Downton Series to the " *Psammosteus* " Limestones, the other (H. W. B.) for the succession upwards from the base of the Clee Series. The description of the Ditton Series above the " *Psammosteus* " Limestones is a combined account. A brief summary of these researches has been published in an excursion guide to the area (Ball & Dineley, 1952).

(c) *Stratigraphical Succession*

LOWER CARBONIFEROUS		
Basal Conglomerate		6–40 ft.
unconformity		
UPPER OLD RED SANDSTONE		
Farlow Sandstone Series		230–510 ft.
Grey Farlow Sandstone Formation	40–300 ft.	
Yellow Farlow Sandstone Formation	190–210 ft.	
unconformity		
LOWER OLD RED SANDSTONE		
Clee Series		900 ft.
Ditton Series		1,200–1,450 ft.
Upper group of marls, silts, sandstones and cornstones	400–550 ft.	
Lower group of marls, sandstones and cornstones	800–900 ft.	
Main " *Psammosteus* " Limestone	0–16 ft.	
Downton Series		1,150–1,250 ft.
Red Downton Formation	1,070–1,100 ft.	
Grey Downton Formation (with Ludlow Bone Bed at base)	80–150 ft.	

II. LOWER OLD RED SANDSTONE

STRATIGRAPHY

The delimitation of the subdivisions of the Lower Old Red Sandstone sequence in the Anglo-Welsh area has long been a source of controversy, and also its junction with the Silurian (see White, 1950*a*). As originally defined by Lapworth (1879–80), the Downtonian comprised the Upper Ludlow Shales, the Ludlow Bone Bed and the Downton Castle Sandstone. Subsequently, the term was used by several authors to embrace differing groups of strata. However, the most generally accepted classification of the Old Red Sandstone has been that of W. Wickham King who divided it into lithological stages. Utilizing Lapworth's term " Downtonian " as defined by Peach & Horne (1899 : 568), King applied it to a succession of purple marls, shales and sandstones overlying the Temeside Shales (1917 : 97, 98). He later (1925) extended it to embrace a great thickness of predominantly marly beds, and referred to it in his table of succession (p. 383) as the " Downtonian or *Anaspida* marls ", though it is not clear from his table whether he regards the Ludlow Bone Bed as forming the base of the " so-called Old Red Sandstones ". Subsequently in the same paper a further name, " Downtonian Series ", was introduced for the same beds. Similarly, the succeeding strata were referred to in the table of succession as the " Dittonian or *Pteraspis* Cornstones " and later as the " Dittonian Series ", the term " Dittonian " having been introduced by King in two earlier papers (1921*a*, *b*). The junction between the Downtonian and Dittonian was designated as the base of the " *Cephalaspis* Sandstone—cornstone", occurring up to 300 ft. above the " *Psammosteus* " Limestones. Above the Dittonian, " Brownstones " were tentatively recorded, with the " Farlow Sandstones " unconformably overlying the Dittonian and the Brownstones.

King (1934) retained the terms " Downtonian " and " Dittonian ", discarding the alternative names, although in his table of succession (p. 527) he referred to the " Downtonian Marls ". Both the Downtonian and Dittonian were regarded as the upper part of the Silurian, the Ludlow Bone Bed being included with the Upper Ludlow. A more recent summary of the Old Red Sandstone succession based largely on King appears in Wills (1948), which notes the " Brownstones " as unconformably overlying the Dittonian, though this is considerably emended in a later edition (Wills, 1950).

The practice of the Geological Survey regarding the subdivision of the Old Red Sandstone has been varied and is summarized by White (1950*a* : fig. 2). Most recently, and with special reference to this area, Whitehead & Pocock (1947) placed the Downtonian-Dittonian boundary at the base of the " *Psammosteus* " Limestones, retaining the Downtonian with the Silurian. The beds below the " *Psammosteus* " Limestones were given the stratigraphical name " Downton Series ", and those above and including the limestones the name " Ditton Series ".

From his researches into the fish faunas of the Lower Old Red Sandstones of the Anglo-Welsh area, White (1950*a* ; White & Toombs, 1948) arrived at similar conclusions, though differing from Whitehead & Pocock on one very important point, namely, the inclusion of the Downton Series with the Old Red Sandstone. He regarded the Dittonian as being marked by the appearance of *Pteraspis*, approximately at the level of the " *Psammosteus* " Limestones.

In Corvedale, one of us (D. L. D.) has found that there is one main limestone horizon which, though showing some lateral variation, can be traced throughout the area. Therefore, with regard to drawing a well-defined marker horizon, the acceptance of the " *Psammosteus* " Limestones as the Downtonian-Dittonian boundary, as proposed by Whitehead & Pocock (1947), is an obvious solution. However, since *Pteraspis* (*Simopteraspis*) *leathensis* White has now been found to occur below the limestones, the boundary does not coincide with that of White's faunal zonation. Nevertheless, it has been amply demonstrated in many fields of palaeontology that faunal assemblages and maxima are more reliable indices than the appearance and disappearance of individual species. Moreover, for this area, the correlation between the faunal and stratigraphical horizons is suggested as being sufficiently close for them to be regarded as broadly contemporaneous.

In the present work the stratigraphical names (i.e. time-rock units) " Downton Series " and " Ditton Series " are retained, whilst the " Downtonian " and " Dittonian " are regarded as denoting the equivalent epochs (time units) within the Lower Old Red Sandstone. The highest part of the Lower Old Red Sandstone sequence occurring in this area is formed by the Clee Series, representing the Breconian epoch.

(a) *Downton Series*

The Downton Series comprises a sequence of 1,150 to 1,250 ft. of predominantly red and purple marls, with thin lenticular sandstones and pellet beds distributed irregularly throughout its middle and upper parts. The Ludlow Bone Bed is here accepted as the base of the Series, whilst the succeeding Ditton Series is regarded as commencing with the main " *Psammosteus* " Limestone (see below). The Downton Series is subdivided into two groups, the lower Grey Downton Formation, corresponding to the Temeside Group of Robertson (1927), and the succeeding Red Downton Formation, equivalent to the " Red Downtonian beds " of Whitehead & Pocock (1947 : 4).

(i) *Grey Downton Formation*

This formation consists of olive, grey and buff flags and shales with occasional purple marls, and is transitional between the shales of the Upper Ludlovian and the marls of the Red Downton Formation. In the Ludlow area the subdivision of this facies into Ludlow Bone Bed, Downton Castle Sandstones and Temeside Beds can be clearly demonstrated (Elles & Slater, 1906), but it is not possible to maintain this subdivision with certainty in Corvedale where the exposures are few and poor. The Ludlow Bone Bed in Corvedale has been mapped by Robertson (1927). No new exposures have been found, whilst some of those examined by Robertson no longer exist and there is no certainty that they all form part of a constant, single stratum ; indeed, Elles & Slater and Robertson recorded more than one bone bed horizon between Ludlow and Much Wenlock. It has not been possible to distinguish the Downton Bone Bed.

Whilst there is no sharp division of the Grey Downton Formation into the members recognized at Ludlow or Much Wenlock, the same general sequence occurs. There is a progressive transition from grey calcareous to red facies :

Lithologies	Ludlow	Corvedale	Much Wenlock
Grey, olive, purple and chocolate mottled shales and mudstones	120 ft.	Generally less than 90 ft.	50 ft.
Thin-bedded pale sandstones. Massive yellow sandstones. Downton Bone Bed (local). Olive sandy shales. Ludlow Bone Bed	30–50 ft.	30–40 ft.	30 ft.

Despite the lack of exposures, it is apparent that thick sandstones are few and impersistent and that the facies change occurs within a maximum thickness of 170 ft. in the south, the thickness decreasing northwards, at least as far as Shipton. From the area around Norton to Diddlebury, the formation decreases from at least 150 ft. to 90 ft. in thickness. Near Hungerford and Broadstone, an estimated 100 ft. of olive shales and chocolate-purple mudstones lie below dark red marls, some of the beds being extremely micaceous. Nothing can be added to previous accounts of the palaeontology.

(ii) *Red Downton Formation*

The red marls and occasional impersistent sandstones constituting this formation outcrop in the low land of Corvedale, the Ledwyche Valley and to the north of Monkhopton and Morville. There is a continuous upward transition and the fossils are rare and confined to highly localized concentrations. In view of this, the limits of the formation are based largely upon lithology. The junction of the Red Downton Formation with the Grey is drawn where the first thick red marls appear and is thus somewhat arbitrarily fixed between exposures in western Corvedale. As White (1950*a* : 54) has suggested, the lowest parts of the red facies may well be coeval in places with part of the grey elsewhere. The main " *Psammosteus* " Limestone (see below) appears to form a mappable horizon about 1,100 ft. above the base of the Red Downton Formation.

The marls greatly resemble those of the Trias and are usually extremely fine-grained, red, chocolate or bluish purple, with frequent green-stained, ramifying bands, spots and joint-planes. Petrographically they are identical with those of the Red Marl Group in the Cardiff district described by Heard & Davies (1924 : 502). Usually there is little trace of bedding or lamination, but the cuboidal jointing on weathered surfaces, characteristic of Triassic marls, commonly occurs. Some horizons, however, include finely laminated, micaceous siltstones. Also associated with the marls are thin bands of small, closely packed, calcareous concretions (" race "), which sometimes take the form of thin, irregular, vertical rods, reaching 4 in. or so in height and ½ in. in diameter.

Thin, lenticular sandstones and pellet beds are irregularly distributed throughout the marl sequence, especially near the base and locally in the middle and upper parts of the formation. In particular, two sandstone developments, the " Holdgate coarse sandstone " and the " *Ischnacanthus* Sandstone ", were defined by King (1925 : 384 ; 1934 : 527) as " stages " of his Downtonian, occurring 815 ft. and about 1,230 ft. respectively above the Ludlow Bone Bed. Subdivision based upon lithology is, however, impracticable in these variable sediments and the scarcity of fossils makes palaeontological zonation equally difficult. Nevertheless, the lowest sandstones of the formation may be equivalent to the " *Thyestes* (*Auchenaspis*) Sandstone " of Ledbury, whilst those at the top are indistinguishable from the Dittonian sandstones. The sandstones are lenticular and vary considerably in colour and grade. They consist largely of subangular or angular quartz grains, with varying amounts of mica, feldspar, accessory heavy minerals and clay minerals with ferruginous or calcareous cements, the latter often showing lustre-mottling. Pellets and flakes of marl are frequently included, sometimes in such profusion that the sandstone grades into a pellet rock. With an increase in calcium carbonate the pellet rocks may in turn grade into a cornstone. Near the base of the " *Psammosteus* " Limestones escarpment several very coarse grits are known, but no pebble beds of the type described by Heard & Davies (1924 : 495) have been found.

Opinions as to what constitutes a " cornstone " vary widely (see Allen, 1960), but as stated by Murchison (1839 : 55, footnote 2), " In the country . . . of the Old Red Sandstone, the name of ' Cornstone ' is restricted to the coarse, sandy, conglomerate-like masses, and is never applied to the large concretions of purer limestone " ; and again a little further on (p. 180), " . . . while at intermediate places [the cornstones] consist of marl, limestone, and sandstone, irregularly concreted, and have the aspect of a conglomerate. In the last-mentioned form alone, they constitute the cornstones of the inhabitants . . . ". Thus, throughout this paper the term will be employed in this context.

Cornstones are most conspicuous in the uppermost Red Downton Formation and the Ditton Series. Generally they are from 1 to 4 ft. thick, though reaching as much as 14 ft. in the Ditton Series. They vary widely in lithology, ranging from relatively pure to gritty and marly limestones, and may be red, purple, buff, grey-green, green or variegated in colour, according to the form and amount of the iron salts present. They are largely composed of fragments of muddy limestone or calcareous marl, commonly rounded or sub-rounded, though occasionally sub-angular, ranging in size from a few millimetres up to several centimetres. Some cornstones consist mainly of one type of pellet or of water-sorted " race ", whilst others also incorporate pebbles of vein quartz, cherts, jasper, and pellets of vegetable carbon. The matrices consist of crystalline and muddy calcite, marl and sand in varying proportions and, when weathered, the beds may assume a nodular or rubbly appearance. Fragmentary

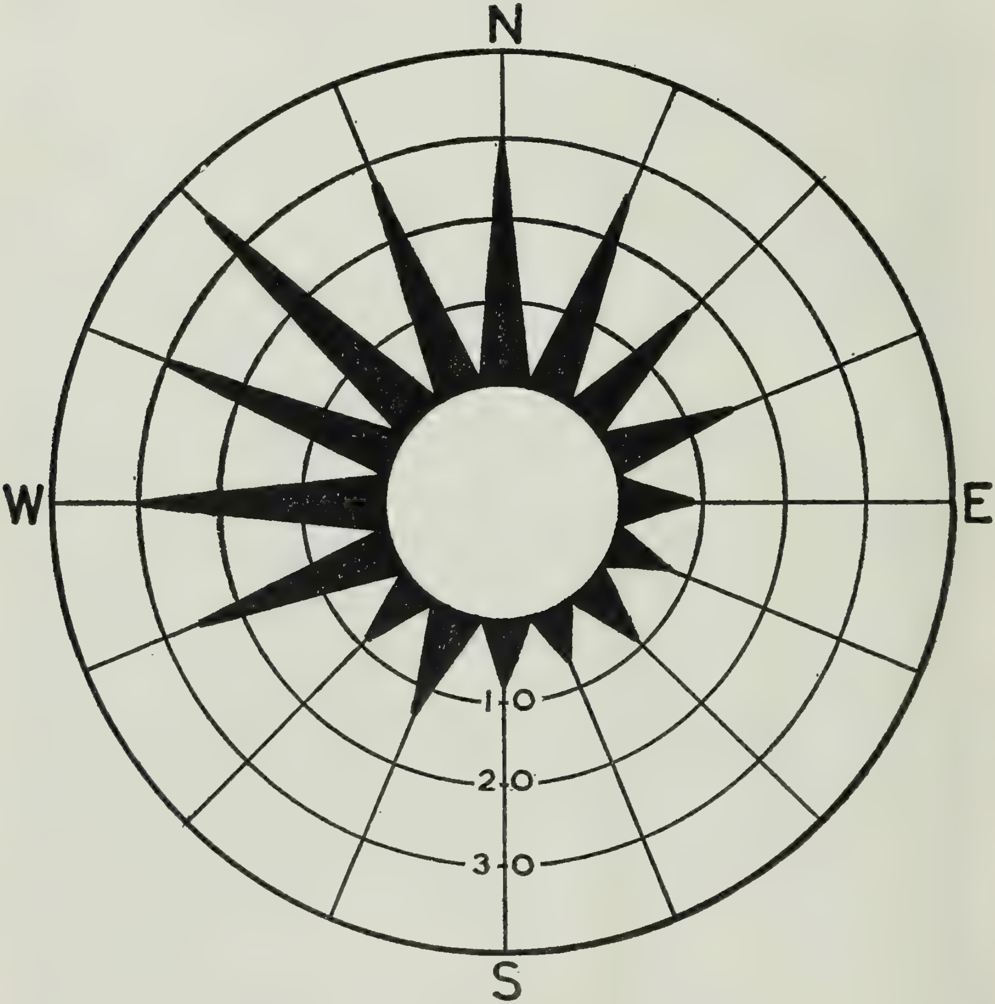


Fig. 1. Current directions as indicated by dips recorded from foreset beds in sandstone and conglomeratic cornstone units within the upper part of the Downton Series and the lowest 400 ft. of the Ditton Series, measured on the northern and western slopes of Brown Clee Hill.

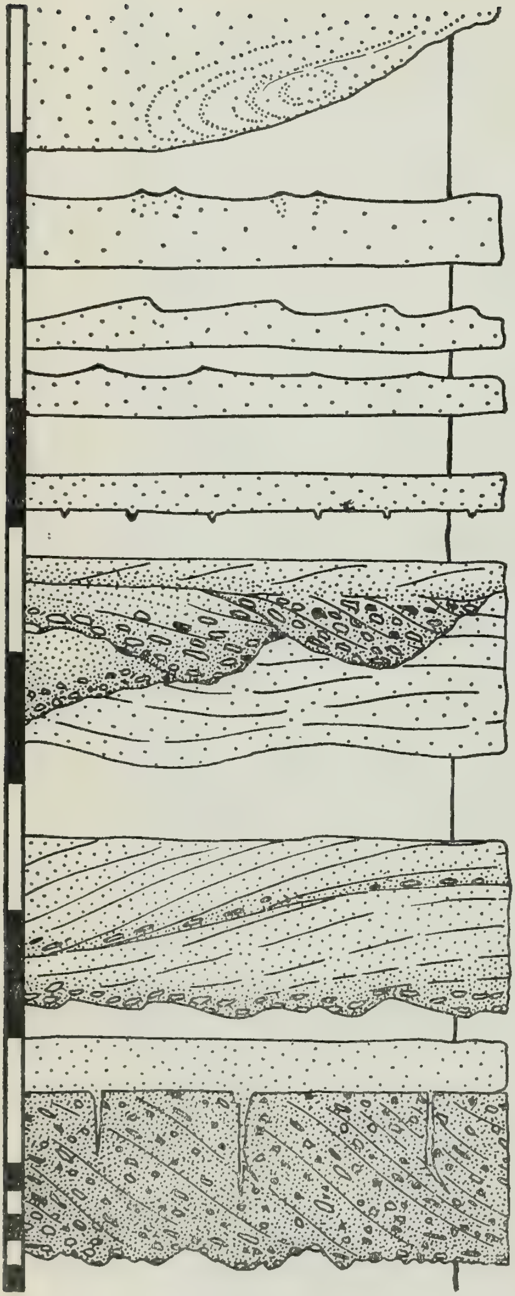
fish remains frequently occur, sometimes in considerable local concentrations. The calcareous bodies ascribed to algae by Heard & Davies (1924 : 505) in the Cardiff district, have not been found in the present area. Many of these beds rest upon highly irregular erosion surfaces, sculptured into the marls to a depth of several inches. Cross-bedding, in which the foreset beds are generally less than 1 ft. thick, is common and some of the thicker cornstones show successively overlapping, short, irregular, cross-bedded lenticles between 1 and 4 ft. thick. A few strikingly cross-bedded cornstones appear as " wash-outs ", cutting locally through the underlying beds to a depth of 3 to 4 ft. From the measurement of some 300 separate foreset bed dips within the uppermost Downtonian and the Dittonian strata, it would seem that the dominant direction of transport was from the north-west (Text-fig. 1), though in any one section the directions may be reversed several times.

Oscillation ripple-marks are common in many sandstones, the crest intervals being usually between 3 and 5 in., though smaller ones are known and shallow marks with crest intervals of 9 in. or more occur upon the upper surface of some cornstones. Current ripple-marks with crest intervals of about 2½ in. have also been found. Small desiccation cracks are present below a number of sandstones, whilst in the Lye Brook and on Titterstone Clee Hill very large ones occur. Vertical sandstone-filled fissures, some 2 ft. deep and ½ in. wide, similar to those noted by Dixon (1921 : 29) in Pembrokeshire, penetrate the upper parts of cornstones at Aston Eyre and near The Alders (Text-fig. 2).

In the Fishmore Brick Pit, Ludlow, in beds which are probably low in the Red Downton Formation, several cross-bedded cornstones are exposed, each about 18 in. thick and 15 ft. long and consisting of poorly sorted, rounded marl pellets and " race ". They rest upon sharp, irregular marl surfaces and appear to represent gravel-filled runnels cut into the marl shortly after its deposition. Desiccation cracks and rain-pit markings occur in a sandstone band, and near the top of the brick-pit section a conspicuous sandstone wedges out sharply, showing near its termination small circular contortions of the bedding, possibly resulting from the slumping of the sediment in a channel incised in the marl (Text-fig. 2).

Near the base of the formation in western Corvedale, scattered, thin, lenticular, red and purple sandstones may represent the " Ledbury Beds " of Worcestershire, but have not yielded any diagnostic fossils. King appears to have established the presence of beds yielding *Thyestes* (*Auchenaspis*) *egertoni* (Lankester) to the north of Morville (Whitehead & Pocock, 1947 : 22). Six feet of closely alternating purple marls and fine ferruginous sandstones, temporarily exposed at Little Thonglands, near Holdgate, greatly resembled the " Ledbury Beds " of Ledbury (Piper, 1898), and pale red and green micaceous sandstones 400 yds. south-east of Brockton have yielded acanthodian spines.

King's stage I. 4, " Holdgate Sandstones ", was stated by him (1925 : 384 ; 1934 : 527) to occur at 815 to 830 ft. above the Ludlow Bone Bed. Subsequently, the term " Holdgate Sandstones Group " was retained for the sandstones near the middle of the Red Downton Formation (Ball & Dineley, 1952). However, there is little to distinguish these sandstones from others within the formation and it is perhaps best to use the term in its purely local connotation, i.e. only for the sandstones in the



Structures in sandstones and conglomeratic corn stones	Localities where structures were noted (List not exhaustive)
1. Lenticular units, slumping of sand down sides of small channels	Ludlow 513754, Stoke St. Milborough 574811.
2. " Spring-pits " . .	Tugford 565872.
3. Ripple-markings, asymmetric . . .	Bouldon 549841, 548840, Hayton 525815, Monkhopton 631926.
4. Ripple-markings, symmetric	Chetton 665901, Monkhopton 633922, Neenton 651871, Silvington 607798, Stanton Lacy 509802, 524778.
5. Desiccation-cracks	Bouldon 541840, Ludlow 513754, Morville 672928, Tugford 565869.
6. " Wash-outs ", scoured and filled channels in sandstone-cornstone units	Bouldon 552854, Hopton Cangeford 530805, Monkhopton 633943, Tugford 555863, Upton Cressett 648932.
7. " Rolling " or " wavy " bedding in sandstones ; undersurface may show tendency towards " flow-casting "	Bouldon 549850, Ditton Priors 606906, Monkhopton 634928, Neenton 653895, Stoke St. Milborough 512816, Upton Cressett 661922.
8. Cross-bedding, foreset beds at Low angles to surface of unit : units with little or no discordance between them	Ditton Priors 586887, Hopton Cangeford 549799, Monkhopton 625926, Silvington 623801, Stanton Lacy 509802.
9. Undersurface, possibly of relief, with non-linear features	Ditton Priors 612904, Middleton Priors 622907, Morville 672929, Stanton Lacy 519778, Tugford 555862.
10. Sandstone with " sandstone dykes " penetrating bed below	Aston Eyre 643932, Stoke St. Milborough 562802.
11. Cross-bedding, foreset beds at high angles to surface of unit. Units may be very irregular in thickness, foreset dips differ in successive units, base marked by erosion surface with sharp relief ; flutings and scour-marks may show preferred orientation	Bouldon 546848, Ditton Priors 610905, Holdgate 574889, Hopton Cangeford 530805, Monkhopton 631927, Morville 671928, Stanton Lacy 510801, Tugford 568877.

Fig. 2. Sedimentary features found in the Downtonian and Dittonian sandstones and conglomeratic cornstones of the Clee Hills area. Argillaceous beds left unstippled, vertical scale in feet.

vicinity of Holdgate village, where the principal sandstone horizon is about 650 ft. above the Ludlow Bone Bed. Sandstone lenses are recorded at many localities throughout central and northern Corvedale and in the country near Acton Round, at a few localities in southern Corvedale, and in the Ledwyche Valley. They are variable in grade and colour and many are very similar to the sandstone from " I. 5 " at Eastham brickworks, near Tenbury, Worcestershire, described by Walder (1941 : 245). The individual lenses are rarely thicker than 15 ft., and are separated by varying thicknesses of marl.

These beds are best developed near Acton Round where relatively coarse sandstones, intercalated with red and green marls, form a distinct feature. They are probably also present north and east of Morville where much of the solid geology is obscured by drift. Between Acton Round and Morville the sandstones are distributed throughout some 400 ft. of strata, the highest occurring 280 ft. below the main "*Psammosteus*" Limestone at Monkhopton. The Beaconhill Brook section shows the typically lenticular nature of the sandstones, many resting upon erosion surfaces cut into green marl. The individual beds are thin and seldom more than 50 yds. long, their basal layers usually containing water-rolled flakes of marl. Strong cross-bedding is general and suggests a predominantly northern derivation. A few local concentrations of fish fragments occur and include *Kallostrakon* and acanthodian remains. Westwards to Skimblescott the sandstones decrease in number, whilst between Skimblescott and Stanton Long only a few very thin friable sandstones have been found. At Holdgate a marked N.–S. scarp is formed by a coarse sandstone or group of sandstones, about 18 ft. thick, the top bed being some 650 ft. above the Ludlow Bone Bed. Further sandstones are developed at this horizon at Baucott, Culmington and Stanton Lacy. In the Ledwyche Valley dark, mottled sandstones occur near Fishmore Hall, Warthill and Brook House.

The uppermost 100 ft. of the Red Downton Formation include further coarse beds, localized in groups near the foot of the "*Psammosteus*" Limestones escarpment. Sandstones and cornstones here alternate with marls and are so similar to the Dittonian beds that they may be regarded as locally developed precursors to those of the Ditton Series. These beds are well exposed in Lye Brook, Morville, where some 100 ft. of strata occur below the limestone, the lowest conspicuous bed being a cross-bedded, white, pellety grit yielding *Traquairaspis symondsi* (Lankester). Above this, lenticular groups of thin cornstones and sandstones are exposed and occupy about 15% of the succession. Several prominent sandstone and cornstone bands can be traced along Meadowley Hill and Aston Hill, some of which have yielded *Pteraspis* (*Simopteraspis*) *leathensis* White; but, with the exception of Lye Brook 4, their exact relationship to the main "*Psammosteus*" Limestone is not certain since some of them are undoubtedly displaced by large-scale hill-creep and may be Dittonian. The cornstone near Yewtree Dingle (121)[1] yielding *Pteraspis* (*Simopteraspis*) *leathensis* White and other fossils, mentioned by White (1950 : 74, 75), is placed by King just below the "*Psammosteus*" Limestone and by Pocock (*in lit.*) 50 ft. above "a *Psammosteus* Limestone". However, each is probably referring to a different limestone, and it seems likely that the lower is the main limestone (see below). A coarse white grit similar to that in Lye Brook outcrops about 100 ft. below the only "*Psammosteus*" Limestone at Stapely Dingle, but the sections in Hudwick and Sudford Dingles, Monkhopton, show only a few thin impersistent sandstones in the red marls below the main "*Psammosteus*" Limestone. A thin red cornstone 25 ft. below the main limestone in Foxhole Coppice, Monkhopton (31), contains *Kallostrakon* and acanthodian remains.

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[1] The numbers in parentheses after localities correspond with those given in the List of Fossil Localities and on the map

Even in closely adjacent sections on the escarpment between Monkhopton and Tugford the successions differ, comparable sequences occurring in two only. The fossiliferous cornstone and underlying marl and "race" outcropping in Earnstrey Brook (25. See Wills, 1935) are exactly like the beds at the foot of the section near Little Oxenbold (51), two miles to the north-east and both horizons yield a rich fauna. Exposures between the two localities show red and green marls with occasional coarser beds. The sporadic outcrop of cornstones suggests restricted accumulation, perhaps in a stream channel.

At Bouldon rapidly alternating red and green shales and thin-bedded argillaceous sandstones and cornstones lie below the main "*Psammosteus*" Limestone. South and east of Bouldon only a few scattered, lenticular, barren sandstones and cornstones have been found near the top of the Red Downton Formation.

(b) *Ditton Series*

The Ditton Series comprises a sequence of closely alternating marls, silts, lenticular sandstones and cornstones, delimited by the main "*Psammosteus*" Limestone at the base and the lower Abdon Limestone above. However, as is pointed out below (p. 198), it may be necessary at some future date to redefine the top of the Ditton Series, since the uppermost 150 ft. may be coeval with the lower part of the Senni Beds (i.e. Breconian) of the Black Mountains, as defined by Croft on the basis of their flora. The Series can be broadly subdivided into two subsidiary groups, though owing to the lack of a mappable marker horizon the boundary between them is arbitrary. The lower group is lithologically similar to the uppermost Downton Series and principally bright red and green in colour. The upper group is more varied and like the lower part of the succeeding Clee Series, chocolate, buff-grey and orange tints being common, whilst many of the beds are strikingly coarse-grained. Thus, the following lithological subdivisions of the Ditton Series are recognized in the Brown Clee Hill area :

	(iii) Upper group of marls, silts, sandstones and cornstones	400–550 ft.
Ditton Series	(ii) Lower group of marls, sandstones and cornstones	800–900 ft.
	(i) Main "*Psammosteus*" Limestone	0–16 ft.
	Total	1,200–1,450 ft.

During the mapping of the area, local names were erected for convenience and applied to the lower and upper groups of the Ditton Series ; "Bouldon Beds" for the lower and " Wheathill Beds " for the upper. It is not proposed that these should be retained. However, the term " Wheathill Beds " was incorporated by Wills (1950 : 24, 30) in a classification of the Old Red Sandstone, though assigned by him to the Breconian owing to the alleged presence of " *Rhinopteraspis dunensis* ". This was due to uncertainty over the status of *Pteraspis* (*Cymripteraspis*) *leachi* originally described by White (1938) and hitherto recognized as a variety of *Pteraspis* (*Rhinopteraspis*) *dunensis* (s.s.), but which must now be treated as a separate species (White, 1950*a* : 56) and sub-genus (White, 1960 : 8). Thus, *Pteraspis* (*Rhinopteraspis*) *dunensis* (s.s.) has not as yet been recorded in the Clee Hills area.

The Ditton Series is best exposed in the several stream courses which drain westwards across the Ditton platform, especially where they cut into the " *Psammosteus* " Limestones escarpment. But even here the sequences are discontinuous, the upper part of the lower group and the upper group being poorly exposed. Hence it has proved impracticable to define a type section. The lowest beds of the lower group include a high proportion of sandstones and cornstones which give rise to a prominent escarpment, the so-called " *Psammosteus* " Limestones escarpment. This well-marked feature extends westwards from Underton, in the north-west of the area, along the eastern edge of Corvedale, to Tar Grove on the south-western margin of the Ledwyche Valley. The upper beds of the lower group include a larger amount of marls and form the broadly undulating surface which constitutes the greater part of the Ditton platform. The upper group incorporates a higher proportion of coarser beds which form the steeper footslopes of Brown Clee Hill and Weston Hill. To the north-west of Brown Clee Hill the Ditton Series has a thickness of 1,200 ft., comprising approximately 800 ft. of the lower group and 400 ft. of the upper. However, to the south-east of the hill the Series thickens to 1,450 ft., consisting of some 900 ft. of the lower group, which also includes more coarser beds in its upper part, and 550 ft. of the upper group. Around the head and eastern margins of the Ledwyche Valley, the " *Psammosteus* " Limestones escarpment merges with the generally steeper slopes resulting from the inclusion of a higher proportion of coarser beds in the lower part of the Series.

Between Brown Clee Hill and the Coal Measures of the Wyre Forest, delimited in the north by the " *Psammosteus* " Limestones escarpment and in the south by the northern slopes of Titterstone Clee Hill and the Farlow-Walton ridge, the Ditton Series forms a broad area of rolling country. Extending north-eastwards around Brown Clee Hill, the outcrops of the subdivisions of the Series expand rapidly, the lower group in general outcropping north of a line from Cleobury North to Deuxhill, the upper group largely occupying the area to the south of this line.

(i) *Main* " Psammosteus " *Limestone*

Since the earliest studies of the Anglo-Welsh Old Red Sandstone were made, the presence of a group of widely distributed, distinctive limestones, the " *Psammosteus* " Limestones, lying immediately above a thick marl division, has been known. Several workers have used them as marker horizons, Whitehead & Pocock (1947 : 7, 8) defining them as demarcating the base of the Ditton Series in the north-east of the area.

McCullough (1870 : 35) noted that one apparently continuous limestone could be traced for some distance in the Pontrilas district. More recently White (1946, 1950*a*) has discussed the derivation, validity and continued use of the name " *Psammosteus* Limestones " and has suggested that they may be diachronous. The general characteristics of their lithology have been described (recent notes have been added by White, 1946 ; Dineley, 1951 and *in* Ball & Dineley, 1952), but a detailed petrographical study is still greatly needed. Fleet (*in* King, 1925 : 385) demonstrated that they are relatively pure limestones and that their inorganic nature seems to be substantiated by the complete absence of fossils.

The distribution of these limestones throughout the Brown Clee Hill area has been mapped with two aims in view, to ascertain (*a*) their reliability as marker horizons, and (*b*) whether they are diachronous. More than one limestone is exposed in several sections on the " *Psammosteus* " Limestones escarpment, but the principal horizon is usually 5 ft. or more thick, reaching 16 ft. at The Hope. The other limestones are generally much thinner, impersistent and nodular, and also more argillaceous and less compact. Where the position of the main limestone was uncertain it has proved possible to locate it with a " Megger " earth-tester, following the technique used by D. W. Gossage whilst mapping the " *Psammosteus* " Limestones near Cleobury Mortimer (Dineley & Gossage, 1959 : 227–229). Elsewhere small excavations have been made to determine the position of the limestone, and at only a few points has no limestone been detected. The " *Psammosteus* " Limestone outcrop given on the map is here regarded as the main limestone.

Two limestones are recorded in a small inlier in Borle Brook, near Criddon Bridge (Pocock & Whitehead, 1947 : 22) and between Underton and Lye Brook, the upper being only poorly developed and continuing westwards to Moor Dingle, rising from 400 ft. O.D. at Underton to 480 ft. at The Lye. The lower limestone outcrops at a number of points along the escarpment between Meadowly and Moor Dingle and attains a thickness of 10 ft. near Monkhopton, but in Hudwick Dingle it wedges out and reappears within a few yards. Both nodular and massive limestone occurs in Sudford Dingle. From Foxhole Coppice to Oxenbold Coppice there is only one limestone, infrequently exposed, but detected by the " Megger " earth-tester and maintaining a constant level at about 700 ft. O.D. No limestone has been detected in Oxenbold Coppice, but from its southern end a thick limestone can be followed southwards between 500 and 600 ft. O.D. into the Ledwyche Valley, rising north-eastwards to 650 ft. near Gibbridge where it is faulted down 90 ft. to the east. A little further to the east, it is downthrown some 150 ft. to the south-east by the Brown Clee Fault, but rises to nearly 800 ft. at Langley, its easternmost outcrop in the valley. South-westwards from Stantongate the limestone reaches an elevation of 900 ft. O.D. on the western flank of Titterstone Clee Hill, then descends to 700 ft. at Bitterly, a mile to the south.

Only one limestone appears to be persistent throughout the Brown Clee Hill area. It is irregular in thickness and locally absent, like a sheet with holes and thin patches. This bed, referred to as the main " *Psammosteus* " Limestone, is here regarded as an important marker horizon, defining the base of the Ditton Series. Thinner, impersistent limestones are locally, but not extensively, developed.

(ii) *Lower Group of Marls, Sandstones and Cornstones*

The best exposures in the lower group of the Ditton Series occur in its lower part, particularly along the streams cutting through the "*Psammosteus*" Limestones escarpment. One of the most continuous sections occurs in the stream draining from Cockshutford to Tugford, where approximately 60% of the exposed strata consists of marls, though the true proportion of these is probably nearer to King's estimate of 70% (1934 : 529). The marls in the lower part of the group are predominantly red and purple in colour, the latter generally being highly micaceous, with numerous layers and lenticles of green marl. Silty marls also occur, particularly in the upper part of the group, and tend to be duller and slightly browner. Both types frequently contain ramifying pipes and veins of purple marl, and erosion surfaces are common where marls are overlain by sandstones. The marls also incorporate lenticles of "race" and variegated, concretionary limestones. Near the top of the group two thin bands of limestone, lithologically identical with the Abdon Limestones, occur near New Earnstrey Park.

The sandstones of the lower group of the Ditton Series are almost invariably fine-grained, though as pointed out by King (1934 : 528) they are generally coarser and much less micaceous than those of the Downton Series. The sandstones are principally red- and purple-brown in colour, with many green bands, and are frequently calcareous and hard, sometimes incorporating sandy, calcareous nodules. They are characteristically current-bedded and frequently show ripple-marked bedding planes, whilst desiccation-cracks, (?) animal tracks, and other trace fossils have also been recorded. Sole markings occur in many of the sandstones and are clearly of more than one type. Most conspicuous are the impressions of erosion surfaces, with small washouts and sandstone piping, but possible post-depositional structures also occur. A few thin bands of coarse grit occur, particularly in the "*Psammosteus*" Limestones escarpment.

Associated with the sandstone bands are lenses of cornstones, commonly composed of pellets of red-brown marl, and red, grey and yellow-buff marly limestones set in a marly, silty or occasionally sandy, calcareous matrix. The size of the pellets varies widely, typically between 0·5 and 1·5 cm. in length, though ranging up to 8·0 cm. Some of the cornstones incorporate angular or sub-angular pebbles of vein quartz, and many include fragments and scales of ostracoderms. Lenses of green cornstones also occur, usually less calcareous than the preceding cornstones, being composed of pellets of green and olive marl, sometimes calcareous, in a green marl or sand matrix. Such cornstones are generally found associated with green sandstones and frequently incorporate small quartz pebbles and carbonized plant remains.

Passing up the sequence, the lower group of the Ditton Series becomes duller and more silty, and the relative proportion of marls increases. King's "*Cephalaspis* Sandstones", present in the Trimpley inlier, cannot be distinguished in the Brown Clee area, and no marker horizons have been detected in the Ditton Series above the main "*Psammosteus*" Limestone. Thus, though both the upper and lower groups have distinctive faunas and in general the upper group is marked by an increase in the amount of sandstones and cornstones, the junction between them is arbitrary.

The best section in the lower part of the lower group occurs in Hudwick Dingle where sandstones and cornstones constitute about 52% of the measured succession of 220 ft., a higher proportion than in other nearby sections.

The junction of marls with overlying sandstones is here usually sharp, frequently uneven, sometimes consisting of an erosion surface beneath which the marls are stained green to a depth of 2 to 3 ft. Cornstones are developed at the base of many sandstones, which are as a whole much less micaceous than the Downtonian sandstones. Cross-bedding is common and oscillation ripple-marks are found in a number of the higher beds. No desiccation-cracks have yet been found in the succession in Hudwick Dingle, but in the lower part bands of " race " and thin argillaceous limestones occur. A thick cornstone immediately above the main " *Psammosteus* " Limestone (37) has yielded a large fauna, including *Traquairaspis symondsi* and *Pteraspis* (*Simopteraspis*) *leathensis*. The latter also occurs at an horizon some 80 ft. higher (39), whilst *Pteraspis* (*Pteraspis*) *rostrata* var. indet. is found at 175 ft. above the limestone (40).

Coarse beds constitute about 43% of the strike section, vertical thickness 100 ft., occurring above the main " *Psammosteus* " Limestone in Borle Brook between Upton Cressett and Wallsbatch, and lying in the zone of *P.* (*S.*) *leathensis*. Several thin sandstones and cornstones are exposed in Rea Brook, which are disrupted by small faults and thrown into small sharp folds, in the vicinity of Middleton Priors.

The outcrop of thick sandstones and cornstones in the lower part of the Ditton Series on the western side of Brown Clee Hill, gives rise to well-defined local features, particularly at Bouldon and Sutton Hill. Stream sections along the " *Psammosteus* " Limestones escarpment between 700 and 800 ft. O.D. expose sequences of rapidly alternating marls, sandstones and cornstones, dipping south-eastwards at 5 to 10 degrees, the marls forming about 60% of the total. Many of the cornstones are extremely coarse containing pellets up to 10 cm. in length. A good section outcrops in Kidnall Gutter, Tugford, where the main " *Psammosteus* " Limestone is particularly well exposed. The Kidnall Gutter section is noteworthy for having yielded *P.* (*P.*) *rostrata* var. indet. from a cornstone 15 ft. above the main " *Psammosteus* " Limestone (44) with *P.* (*S.*) *leathensis* occurring a further 15 ft. above (45). The stream bifurcates in its upper reaches and the contrast between the two resultant sections illustrates the rapidity of lateral change within the beds. This is also well shown in Oak Dingle (75), Tugford, where a green cornstone-sandstone, estimated to lie about 125 ft. above the main " *Psammosteus* " Limestone, has yielded *Pteraspis* (*Pteraspis*) *rostrata* var. *trimpleyensis*, *Traquairaspis symondsi* and *Tesseraspis*. Several small structures resembling spring-pits (Shrock, 1948 : 136) occur in a sandstone at the foot of the section.

The sections in Clee and Abdon Brooks are poor, the scattered exposures largely consisting of red and green marls with a few green sandstones and cornstones. Old quarries on the escarpment near Bouldon expose sections in buff and olive shales and sandstones and extremely coarse cornstones. A cornstone exposed in Clee Brook at Bouldon (13) about 50 ft. above the main " *Psammosteus* " Limestone, has yielded *Pteraspis* (*Pteraspis*) *rostrata* var. *trimpleyensis*, whilst a very coarse cornstone outcropping in the Old Forge Quarry (77), Bouldon, is possibly the same as that occurring 24 ft. above the main " *Psammosteus* " Limestone in Strand Brook, three-quarters of a mile to the south. The quarry at Hoptongate (36) shows an exceptional sequence of 8 ft. of green, argillaceous cornstone in thin, successive, cross-bedded lenticles, many of which have truncated upper surfaces. The fine section in Tar Grove Quarry (105), east of Whitbatch and about 175 ft. above the main " *Psammosteus* " Limestone, has yielded *P.* (*P.*) *rostrata* var. *trimpleyensis* and *T. symondsi* from the same stratum, this being the highest record of the latter.

The middle and upper parts of the lower group are poorly and intermittently exposed in stream sections to the west of Brown Clee Hill, and in Ledwyche Brook and Newton Dingle near whose confluence thick sandstones and cornstones occur. The beds are sparsely fossiliferous, but have yielded *P.* (*B.*) *crouchi*, *P.* (*P.*) *rostrata*, *P.* (*P.*) *dairydinglensis* and arctolepids. Bright red and green marls with thin cross-bedded sandstones and cornstones of the lower group outcrop in the " saddle" between Bromdon and Titterstone Clee Hill and extend eastwards into the Silvington Valley where they have yielded *P.* (*B.*) *crouchi*. There appears to be considerable faulting in this region and the exact thickness of the lower part of the Ditton Series here is uncertain.

The lower group of the Ditton Series equates with the *leathensis* and *crouchi* Zones.

(iii) *Upper Group of Marls, Silts, Sandstones and Cornstones*

The transition from the lower group to the upper is marked by a sharp break in fauna, though further intensive collecting may prove that the faunal dichotomy is not so distinct as that implied by present evidence. Furthermore, there is an increase in the proportion of sandstones and cornstones, and also in the coarseness of grade, marls being replaced to a large extent by silts and silty shales, whilst the upper beds become red-brown brown-buff and grey-green in colour. The trend in increasing coarseness of grade upwards in the succession, shown by the Downton Series and the lower group of the Ditton Series, is continued in the upper group of the latter. Thus, in the lower part of the upper group, marls and silts predominate over sandstones and cornstones. However, the proportion of the latter increases in the upper part and yellow- and brown-buff silts become increasingly common.

The marls of the upper group are predominantly chocolate and green in colour ; the silts are red-brown, buff, grey and green, frequently laminated, and often incorporate sandy, calcareous concretions, nodules of argillaceous limestone and purple " piping ". The sandstones are largely fine-grained or silty and predominantly red-brown, grey, chocolate and pale-buff or green in colour. Some of the sandstones are calcareous, hard and thickly bedded, whilst others are laminated and silty, incorporating scattered marl pellets and sandy, calcareous concretions. Current-bedding is common and many of the sandstones are markedly lenticular. Cornstones are most common in the upper group and show considerable variation in lithology. They frequently have a yellow-buff hue, though they are also red, green and grey, being composed of pellets of yellow-, orange- and chocolate-buff, red-brown, grey and purple calcareous marl and argillaceous limestone. The matrices vary from argillaceous or sandy limestone, which has sometimes become recrystallized, to marl, when the boundaries of individual pellets are frequently difficult to distinguish. The pellets are largely sub-rounded to sub-angular and average 1 to 2 cm. in size, though ranging up to 7 cm. The cornstones are commonly current-bedded and well sorted, the pellets in any given band being of approximately the same size. Some consist of rapidly alternating well- and poorly-sorted lenses, the latter usually being much more marly than the former. The green cornstones are frequently very argillaceous and rubbly, and incorporate much carbonaceous plant debris. A few thin, grey, concretionary limestones occur which are lithologically similar to the " *Psammosteus* " Limestones.

The outcrop of the upper group of the Ditton Series occupies the broad and undulating area to the east of Brown Clee Hill, approximately between Upper Overton and the Farlow-Walton ridge, and forms the footslopes of Brown Clee Hill and Weston Hill. Exposures in the group are few and poor, being either short, discontinuous sections along stream courses and road cuttings, or small isolated quarries. The best section occurs along Bensons Brook, Titterstone Clee Hill, which lies outside the area being described ; but within the area, the most complete section is exposed in Newton Dingle on the southern slopes of Brown Clee Hill. In Newton Dingle, in the area of The Gore, a succession of marls, laminated siltstones and cornstones outcrops, two of the cornstones having yielded *Pteraspis* (*Cymripteraspis*) *leachi* White and, in one instance, *Protaspis* (*Europrotaspis*) *crenulata* sp. nov., whilst plant fragments occur at several horizons in laminated siltstones and sandstones. North of The Gore, the sequence is less well exposed but includes purple, green and buff, silty sandstones and siltstones, with a few bands of rubbly cornstone.

The thick bands of cornstone and sandstone, characteristic of the group, give rise to prominent features such as The Thrift, the col which links Brown Clee Hill with Weston Hill, and the succession of small escarpments in the Wheathill-Silvington area. The scarp slopes face north-west and an outcrop near the top of the slope occurring 1,200 yds. north-east of Silvington (93) reveals a massive cornstone, some 14 ft. thick, dipping to the south-east. Sections in sandstones and cornstones also occur in road cuttings at Clee St. Margaret, Stoke St. Milbrough, Wheathill and north of Farlow Bank. Cornstones at several localities have yielded the characteristic fauna of *Pteraspis* (*Cymripteraspis*) *leachi* and *Protaspis* (*Europrotaspis*) *crenulata*, with numerous arctolepid fragments, and a notable locality (8) near to Besom Farm has yielded *Benneviaspis salopiensis* sp. nov., the youngest cephalaspid yet recorded in this area (see p. 282 ; also Ball & Dineley *in* Whittard, 1953 : 249, 250). Many of the laminated siltstones have yielded plant fragments, though these are poorly preserved and largely indeterminable. However, the late W. N. Croft was able to recognize *Prototaxites*, *Pachytheca*, leaf-like patches of *Nematothallus* and slender branched axes, cf. *Cooksonia*, from an assemblage collected from a small outcrop in silty sandstones at Dodshill Bank (23), half a mile to the south of Besom Farm.

The top of the upper group is exposed in a small quarry 200 yds. north of Walton (114), where the lower Abdon Limestone, which forms the base of the Clee Series, is interbedded with some 15 ft. of sandstones and cornstones. The sandstones include grey and chocolate-grey, massive, hard bands and also buff, silty beds ; whilst the cornstones are red- and green-grey in colour and very gritty, that immediately below the Abdon Limestone having yielded to King a fragment of an arctolepid and an acanthodian scale, the highest record of ostracoderms in the area.

The upper group of the Ditton Series equates with the zone of *Pteraspis* (*Cymripteraspis*) *leachi* White.

(c) *Clee Series*

The base of the Clee Series is here defined as the bottom of the lower of two major limestone horizons which, with the intervening strata, form a prominent feature around the north-western slopes of Brown Clee Hill. This lower limestone horizon is a fairly consistent and mappable feature, and below it the beds are, in general, more typically Dittonian in aspect than those above which rapidly assume the characteristic Clee Series lithology. The upper limestone is also relatively persistent and lies some 200 ft. above the lower. Since both limestones are especially well developed in the area of Abdon where they have been extensively quarried in the past, King has called them (*in lit.*) the Abdon Limestones, and this name will be retained here.

Both horizons show rapid lateral and vertical variations in lithology, from massive to nodular limestones, and calcareous marls somewhat like the " race " of the Downton and Ditton Series. The massive limestones are generally dark brown and brown-purple in colour when fresh and often include a few angular grains of quartz averaging 0·2 mm. in size, with rarer grains of plagioclase feldspar, microcline, tourmaline, zircon, garnet, muscovite, cherts and " felsite ". With an increase in arenaceous material the limestone passes into calcareous and frequently lustre-mottled sandstone. Variations of the massive limestone facies also occur. Much of it appears to have been deposited as a relatively homogeneous calcareous mud showing in thin section signs of movement in a plastic state. Another common variation consists of angular, brown, grey and brown-purple limestone fragments ranging up to 10 cm. in size, set in a like matrix, possibly originating from the pene-contemporaneous breaking up of thin sheets of calcareous mud with rapid re-cementation. The third variation appears to be concretionary in origin (cf. the " *Psammosteus* " Limestones) and sometimes distinctive problematical structures (p. 198) are found associated with it. With an increase of marl and silt the concretionary limestones pass into the nodular facies and ultimately into a calcareous marl, both commonly variegated.

Concomitant with rapid changes in facies, the limestones vary in thickness. The greatest development appears to be along the lower slopes of Brown Clee Hill above Abdon, where the lower limestone is at least 10 ft. thick, Murchison (1833 : 473) recording a thickness of 18 to 20 ft. The outcrop is marked by a succession of small quarries (Murchison, 1839 : 179, 180) now largely overgrown, which extend round the foot of the hill to a point near Hillside Farm, where the limestone is very nodular and marly, and interbedded with lenses of calcareous marl and red-brown calcareous sandstone, or white, lustre-mottled sandstone. To the south of Abdon Liberty the outcrop of the lower horizon is marked by a number of smaller workings which become more sporadic towards Cockshutford, where the limestone is frequently replaced by calcareous sandstones, often white and lustre-mottled. South of Nordybank it appears to be intermittently replaced by calcareous sandstones as far as Pel Beggar, where the limestone becomes re-established in its nodular facies and can be traced eastwards to the south of Bockleton Court. To the south-west of Pel Beggar, a small outlier of the lower limestone caps Weston Hill. At Bockleton Court both horizons are displaced to the south by the Brown Clee Fault, but owing to solifluction the outcrop of the lower is difficult to trace east of the fault, though it is in part marked by overgrown workings and outcrops in the track leading to Shortwood. Nowhere beyond this point along the eastern side of the hill has the lower limestone been detected. Thus the base of the Clee Series on the eastern slopes of Brown Clee Hill has been extrapolated and is wholly conjectural.

The upper limestone, whilst not reaching the thickness of the lower at its maximum, undergoes similar variations in thickness and lithology, and is much more persistent. At Abdon Liberty and along the northern slopes of the hill, the upper limestone forms a prominent rib above the quarries in the lower, and has itself been quarried on a small scale. The trace of the outcrop becomes less pronounced on the north-eastern slopes of the hill, where the limestone becomes more nodular and marly, as can be seen in the old workings at Cleobury North Liberty. South of Abdon Liberty the outcrop is marked by further small workings, whilst between Cockshutford and The Sands the upper limestone has been quarried on a scale commensurate with that of the lower limestone workings on the northern slopes of the hill. The best exposure in the Abdon Limestones occurs in the upper horizon at Cockshutford where it has been exposed by recent quarrying. The upper limestone outcrops in small workings to the north of Bockleton Court where it is displaced to the south by the Brown Clee Fault. East of Bockleton Court it forms a prominent feature which extends round the south-eastern slopes of the hill to Banbury, having been extensively quarried near The Toot. Like the lower limestone, the upper has not been detected on the eastern side of Brown Clee Hill between Banbury and Cleobury North Liberty.

The strata between the Abdon Limestones consists largely of sandstones and silty shales, predominantly red-brown at the lower levels, becoming increasingly buff and grey in colour upwards, which with the limestones form a distinct feature at the foot of the northern and western slopes of Brown Clee Hill. The sandstones are composed dominantly of quartz, both igneous and metamorphic, the grains being largely sub-angular to angular but also sub-rounded and occasionally rounded. The grains range in size from 0·01 mm. (fine silt) to 0·1 mm. (coarse sand) but average between 0·1 and 0·4 mm. (fine to medium sand) ; most of the sandstones being moderately well sorted. Also incorporated are frequent grains of plagioclase feldspar in the albite-oligoclase range, myrmekite, perthite and microcline, and fragments of a variety of rock types including " felsite ", basalt, volcanic glasses, quartz schist, cherts and calcareous marls. The feldspars are largely fresh but some are undergoing sericitization. Accessory minerals include worn zircons, white mica, chlorite, tourmaline, garnet and epidote. Cementation is largely by calcite or ferruginous mud. In some of the calcareous sandstones, the component grains do not form a mesh and were probably deposited by lime-rich waters as a sandy, calcareous mud which has undergone subsequent recrystallization. Some of the quartz grains have been strained and fractured during recrystallization, whilst others have been partially replaced by calcite. Intercalated with the sandstones and silts are lenses of massive and nodular limestones identical with the Abdon Limestones, and variegated calcareous marls.

Succeeding the Abdon Limestones are some 700 ft. of strata consisting largely of sandstones and silts (estimated 85 to 90%) and forming the greater part of the Clee Series. The sandstones are commonly current-bedded and predominantly grey, buff, brown and purple in colour, and though similar in composition to those between the limestones they tend to be coarser, with grain size averaging 0·4 to 0·75 mm. The succession as a whole becomes coarser upwards, with the appearance in the upper part of coarse sandstones and grits.

A large number of the sandstones incorporate pellets and pebbles of variegated calcareous marls, many of which cannot be matched with the marl bands intercalated with the sandstones. The pellets are typically between 1 and 6 cm. in size, but range up to 16 cm., and occur throughout the succession. In contrast, pebbles of vein quartz, yellow and liver-coloured quartzite and cherts are especially common in the upper part of the Clee Series. A derived Silurian polyzoan, *Fistulipora* sp., was found as a pebble in the lower part of the Clee Series at the head of Batch Gutter, 320 yds. north-west of The Toot, but it has not proved possible to assign it to an horizon within the Silurian. Though predominantly sub-angular, some rounded pebbles do occur, and these are usually less than 3 cm. in size. However, like the constituent grains of the sandstones, the pebbles increase in size upwards in the succession, one pebble of 22 cm. having been found in the upper part of the Clee Series. A few bands are entirely composed of pellets and fragments of grey and green calcareous marl with small pebbles of vein quartz, and are comparable with the cornstones of the Downton and Ditton Series. Intercalated with the sandstones are occasional lenses of silty marl, usually purple and green in colour, and variegated, calcareous, nodular marls, some of which grade into nodular limestones similar to the nodular facies of the Abdon Limestones. Rapid lateral facies variation and lensing-out of beds is characteristic of the group as a whole, though many of the strongly developed sandstones in the upper part of the Clee Series are more persistent and form a succession of well-marked features along the western slopes of Brown Clee Hill.

The Clee Series is best exposed along the streams draining the western and south-western slopes of Brown Clee Hill. The most continuous section occurs along the stream course extending north-westwards from Clee Burf to Cockshutford, whilst other relatively good, but more broken sections, can be seen along the streams flowing westwards from Five Springs and south-westwards from Warren Cottage. Numerous small exposures occur on the northern, western and southern slopes of the hill, but are almost entirely lacking on the east. The full development of the Clee Series is not seen since it is sharply truncated by the plane of the Coal Measures unconformity, but its maximum thickness as exposed on the western slopes of Brown Clee Hill is calculated to be 900 ft.

A further small outcrop of the Clee Series occurs as a downfaulted wedge at Walton, in the south-east of the district. A limestone some 3 to 4 ft. thick outcrops in a small quarry 200 yds. to the north of Walton, (114). It is identical with the massive facies of the Abdon Limestones and containing, in addition, the same distinctive problematical markings. The line of outcrop of a similar limestone was revealed by deep ploughing in fields to the south of Walton. Since the latter is calculated to be some 200 ft. above the first limestone it seems probable that they represent the Abdon Limestones. The associated sandstones and silts show a typical Clee Series lithology.

The Clee Series has, as yet, yielded no indigenous fauna or flora. However, as has been stated above, certain problematical markings appear to be confined to the Clee Series, occurring in the Abdon Limestones, in some of the sandstones between them, and continuing at least into the middle of the Series. The markings are identical with those first noted by Croft (Pocock, Brammall & Croft, 1940 : 55) as " pepper-pot " markings in the Senni Beds and subsequently recorded by him as " distinctive problematical structures " confined to these beds and occurring throughout the Black Mountains and neighbouring areas (Croft, 1953 : 431). Despite this absence of diagnostic fauna or flora from the Clee Series, there are strong stratigraphical grounds for correlating them with the Senni Beds of South Wales. Both show similar gradational changes from the Dittonian strata which they overlie conformably (Croft, 1953 : 429), with an increase in the proportion of sandstones and change in colour from predominantly reds and purples to greens and greys. Moreover King has long recognized the close similarity between the Abdon Limestones and the Fynnon Limestones of the Black Mountains. In both areas there are two major limestone horizons separated by some 200 ft. of strata, and all are lithologically alike (King *in lit.*).

It should be noted that the base of the Clee as defined above does not correspond with that of the Senni Beds as defined by Croft (*in lit.*), which is at the bottom of a prominent group of sandstones containing a typical Senni Bed flora (Croft & Lang, 1942) extending a short distance below the lower Fynnon Limestone. As yet, the equivalent strata occurring below the Abdon Limestones have not yielded a flora, but if the correlation between the Abdon and Fynnon Limestones can be substantiated and they are not diachronous, it will be necessary to re-define the top of the Ditton Series. Similarly it has been impossible to draw an upper limit to the Clee Series corresponding with the Senni Beds-Brownstones boundary in the Brecon Beacons. Thus it is expedient to retain for the Shropshire Breconian strata the local name of Clee Series until a more exact correlation is possible.

The presence of true Brownstones, namely, strata succeeding the Senni Beds and underlying the Farlovian (Croft, 1953 : 429), cannot be proved in the Shropshire area. But since Croft gives a thickness of 850 ft. for the Senni Beds in Breconshire, and in view of the general correlation between the Clee Series and the Senni Beds, the Brownstones may well be represented by the highest beds of the Clee Series on Brown Clee Hill. The " Brownstones " previously recorded in the area (King, 1925 : 383, 388 ; Edmunds & Oakley, 1947 : 27 ; Whitehead & Pocock, 1947 : 23, 24 ; Pocock & Whitehead, 1948 : 66 ; Wills, 1948, 1950) have proved to be largely of Upper Dittonian age and, in part, lower Breconian. White (1956 : 5) has suggested that the Senni Beds are probably of Middle to Upper Siegenian age, which is therefore true for the Clee Series.

FAUNA AND FLORA

The Downton and Ditton Series are largely barren, though there are a few relatively fossiliferous horizons, particularly the cornstones and sandstones associated with the " *Psammosteus* " Limestones. The fossils are frequently concentrated into lenticles, sometimes forming veritable bone beds. The major part of the fauna consists of ostracoderms, invertebrates being rare, especially in the Ditton Series. The associated flora is poorly preserved. With the possible exception of the problematical structures they contain, the Clee Series appear to be entirely barren.

(a) *Vertebrates*

The Lower Old Red Sandstone of the Clee Hills area has long been known for its ostracoderm fauna, notable collections having been made in the last century by G. Cocking, Rev. J. F. Crouch, Dr. J. Harley, Rev. T. T. Lewis, R. Lightbody, Dr. T. Lloyd, A. Marston and H. Salwey ; and more recently by Dr. E. I. White, H. A. Toombs, Prof. L. J. Wills, and especially the late W. Wickham King. The localities yielding ostracoderm remains are recorded on the map and are listed below. Many of the classic localities which yielded rich faunas in the past now appear to be completely barren, e.g. Whitbach, near Ludlow, which was re-excavated for the 1948 International Geological Congress Excursion C.16, and yielded not a single fragment.

The number of forms present in the fauna is large, and the writers are greatly indebted to Dr. E. I. White for the faunal determinations and for his description of the new forms which it contains. The delicate and laborious preparation of the material has been undertaken by Mr. H. A. Toombs utilizing the acetic acid technique (Toombs & Rixon, 1959). This has revealed incidentally that some of the cornstones incorporate a rich and diversified micro-fauna.

Mode of Occurrence of the Vertebrate Fauna

In his description of the remarkable faunule at Wayne Herbert, Herefordshire, White (1935) was among the first to appreciate the necessity of carefully evaluating the mode of occurrence of ostracoderm faunas. His later studies also emphasized the peculiar nature of the distribution and composition of these faunas, and he suggested (1950*a* : 57, 58) that the vertebrate faunas (faunules) are spasmodic introductions from a plexus of streams emptying into a common basin. This is substantiated by the occurrences in the Clee Hills area, thus :

1. the ostracoderm remains are usually concentrated into small lenticles ;
2. the fossils most frequently occur in cornstones which rest on erosion surfaces and show signs of rapid deposition ;
3. most of the remains are fragmentary, complete and undamaged carapaces being very rare ;
4. the remains are frequently concentrated into residues of fragments of a similar size, buoyancy or weight;
5. the composition of each faunule tends to be distinctive and unique.

As noted above, the cornstones are generally the most fossiliferous, the sandstones being less so, whilst at only two localities have ostracoderms been found in marls.

The largest and most complete remains are frequently found in the bottom few inches of a cornstone, though they are often distorted and damaged by compression and compaction. The base of a conglomeratic, coarse, white grit at Lye Brook, which rests upon an erosion surface, has yielded the following fragments of *Traqairaspis symondsi* :

Dorsal shields . . .	4 relatively complete. 4 large fragments.
Dorsal spines . . .	26 fragments.
Ventral shields . . .	13 relatively complete. 17 large fragments.
Lateral plates . . .	13 relatively complete.
Orbital plates . . .	12 relatively complete.
Rostrum	1 incomplete.
?Branchio-cornual plate .	3 incomplete.
?Pineal	1 incomplete.
Scales (flank) . . .	2.

A number of small fragments were also incorporated, as well as *Tesseraspis*, *Kallostrakon*, and acanthodian spines. In the finer sediments above, only very rare small fragments occur. At least 26 individuals are represented, but only 8 dorsal shields and 1 rostrum are incorporated. It is probable that this selective concentration has been effected by current action. At Netchwood Common (62), 36 rostra of *Pteraspis* (*Belgicaspis*) *crouchi* were collected from about 8 sq. ft. of a cornstone 8 to 10 in. thick, though an even more remarkable concentration of plates has been recorded by White (1938 : 102) in Carmarthenshire.

Wills (1948 : 28) and White (1950 : 73) commented upon a cornstone slab from Morville which incorporated 30 dorsal and 3 ventral shields of *Pteraspis* (*Simopteraspis*) *leathensis*. The lithology of the cornstones suggests rapid deposition and supports White's hypothesis of a fluviatile deposition rather than Wills' suggestion of accumulation in a pool. White further notes that a more or less uniform orientation of plates may occur on a bedding plane, which also suggests transport in, and by, continuously moving water currents.

Most of the larger pteraspid fragments are of dorsal or ventral shields ; branchial and other paired plates may occur intact or broken, yet still attached to the shield, and where detached they are usually imperfectly preserved. The fragments usually show little sign of post-mortem attrition, and where abrasion is present it appears to have occurred during life on those parts of the plates which would be expected to come into contact with the river bed. No complete specimens as recorded by White (1935 : 383) at Wayne Herbert, Herefordshire, have been found. There, the evidence suggested essentially quiet deposition, possibly in a pool. Ostracoderm remains occurring in the finer sediments of the Clee Hills area are rare and usually fragmentary, the fossiliferous marls at Earnstrey Brook (25) and Little Oxenbold (51) being exceptional.

A remarkable feature of the traquairaspid and pteraspid faunules is that each is composed of individuals which are at approximately the same stage of development though they may show some degree of variation in form. Moreover, only rarely is one species of *Pteraspis* found in association with another, which may imply that the species occupied different ecological zones (see p. 252).

Utilizing the pteraspid faunas, White (1950, 1956) has erected a zonal sequence which has enabled the correlation of the Lower Old Red Sandstone of the Anglo-Welsh area with that of the continent. The present research has facilitated the more accurate definition of the limits of these zones within the type area, and the establishment of characteristic zonal assemblages. However, in view of the range within the type area of *P. rostrata* and also of its confused taxonomic status (see p. 247), White's zone of *crouchi* and *rostrata* is here referred to as the zone of *crouchi*. Moreover, it should be noted that throughout this work where reference is made to *Pteraspis* (*Pteraspis*) *rostrata* Agassiz, this does not indicate that the specimen referred to is *rostrata* s.s., but instead, *rostrata* var. indet.

(b) *Succession of the Vertebrate Fauna*

(i) *Downton Series, Red Downton Formation*

Zone of *Traquairaspis symondsi* (Lankester)

Of the small number of fossiliferous localities found in the Red Downton Formation, the great majority occur within the top hundred feet, being associated with the sandstones forming the lower slopes of the " *Psammosteus* " Limestones escarpment. White (1946 : 214 ; 1950 : 55 ; White & Toombs, 1948 : 5) has shown that the upper part of the Downtonian can be subdivided into two zones, a lower with *Traquairaspis pococki* and an upper with *T. symondsi*. However, since the two species occur together near Clifton-on-Teme, and *T. symondsi* has been found 100 ft. below, and *T. pococki* 17 ft. below what is considered to be the same limestone horizon at Gardners Bank (Dineley & Gossage, 1959 : 232), it is evident that the two forms overlap. Their mutual exclusiveness within the zone of overlap (with the exception of Clifton-on-Teme) may indicate, as in the pteraspids, that they occupied different environments.

Only *T. symondsi* has been found in the Brown Clee Hill area. It occurs at five localities, the lowest, Lye Brook (55), being 125 ft. below the main " *Psammosteus* " Limestone, which broadly accords with White's (1950*a* : 55) suggestion of a thickness of up to 150 ft. for the zone of *T. symondsi*. Below this level the sandstones and cornstones are largely replaced by marls, and it seems probable that the zone of *T. pococki* is represented by unfossiliferous strata.

The fauna associated with the zone of *Traquairaspis symondsi* has been recorded by White (1950*a* : 56) as comprising *Anglaspis*, *Corvaspis*, *Tesseraspis*, *Didymaspis*, *Cephalaspis*, *Ischnacanthus*, *Onchus*, *Onychodus*, *Kallostrakon*, *Thelodus*, to which must be added a single anaspid scale from Targrove Dingle 6 (104. See also Woodward, 1948). Most of the elements of the fauna occur in the *pococki* Zone, or in the succeeding zone of *Pteraspis* (*Simopteraspis*) *leathensis*. However, both *Corvaspis* and *Anglaspis* appear in the *symondsi* Zone and, near the top, *P.* (*S.*) *leathensis* and *Poraspis*, in association at New Inn 1 (71) ; whilst *Kallostrakon* does not appear to extend beyond it. Thus, the faunal assemblage characteristic of the *symondsi* Zone is *T. symondsi*, *Corvaspis*, *Anglaspis*, *Tesseraspis*, *Ischnacanthus wickhami* (see pp. 262–264) and *Kallostrakon*.

(ii) *Ditton Series*

Zone of *Pteraspis* (*Simopteraspis*) *leathensis* White

The base of the Ditton Series is marked by a distinctive lithological feature, the " *Psammosteus* " Limestones, and an important faunal change, the replacement of *Traquairaspis* by *Pteraspis* (White, 1950*a* : 56). Although *P.* (*S.*) *leathensis* occurs below the " *Psammosteus* " Limestones, and *T. symondsi* just persists into the bottom of the zone of *P.* (*B.*) *crouchi*, as can be seen from Table 1, *T. symondsi* is largely concentrated below the limestones and is rare above them (see also White, 1950*b*: 74). A further important form occurring with *P.* (*S.*) *leathensis* is *Pteraspis* (*Pteraspis*) *rostrata* var. *trimpleyensis* White, which appears about the middle of the *leathensis* Zone and persists into the lower part of the succeeding zone of *P.* (*B.*) *crouchi* ; moreover *P.* (*P.*) *rostrata* var. indet. occurs near the base of the *leathensis* Zone at Kidnall Gutter, 1 (44).

The earliest arctolepid (cf. *Kujdanowiaspis* sp.) in the area is recorded from the bottom of the *leathensis* Zone, at Criddon Bridge (19).

In addition to these, the fauna associated with the *leathensis* Zone is relatively large (White, 1950*a*), consisting of *T. symondsi*, *Corvaspis*, *Anglaspis*, *Poraspis*, *Tesseraspis*, " *Ischnacanthus* ", *Gomphodus*, *Onchus*, *Cephalaspis*, and acanthodian and thelodont scales. Several of these forms occur in the preceding and succeeding zones, but the assemblage which may be regarded as typical of the *leathensis* Zone is *P.* (*S.*) *leathensis*, *P.* (*P.*) *rostrata* var. *trimpleyensis*, *Tesseraspis*, *Poraspis*, and *Anglaspis*.

The highest locality from which *P.* (*S.*) *leathensis* is recorded is about 110 ft. above the main " *Psammosteus* " Limestone (16. Clapgate Cottage Quarry), whilst the lowest occurrence of *P.* (*B.*) *crouchi* is about 170 ft. above the limestone (98. Sudford Dingle 2). Thus, there is a gap of some 60 ft. between the two, and pending further information regarding the range of these species, the *leathensis* Zone is here regarded as extending 140 ft. above the main " *Psammosteus* " Limestone. The provisional determination of *P.* (*S.*) *leathensis* for small pteraspids from Hopton Brook given by Dineley & Gossage (1959 : 232), has now been verified by Dr. White. However, though recorded as occurring 250 ft. above the " *Psammosteus* " Limestone, it is now evident that owing to faulting their position relative to the " *Psammosteus* " Limestone is uncertain.

Zone of *Pteraspis* (*Belgicaspis*) *crouchi* Lankester

The *crouchi* Zone is poorly fossiliferous, including much barren marls and silts. However, its onset is marked by a further important faunal change in that some of the heterostracans which constitute such a significant element in the faunas of the preceding zones persist only into the lowest part of the zone, being replaced by new forms at a slightly higher level. The former include *P.* (*P.*) *rostrata* var. *trimpleyensis* as well as *P.* (*P.*) *rostrata* var. indet., *T. symondsi*, which occurs at the very base, ? *Corvaspis*, and *Poraspis* (though it should be noted that *Poraspis sericea* probably extends well into the *crouchi* Zone in Herefordshire and Monmouthshire). Although *Anglaspis* is largely confined to the preceding zones, its occurrence at Clee

St. Margaret (17) demonstrates its persistence into the upper part of the *crouchi* Zone, and *Tesseraspis* is noteworthy for also extending into the middle of the zone.

New forms which appear in the zone include *Weigeltaspis* and *P.* (*P.*) *rostrata* var. *waynensis*, in the lower part, *Pteraspis* (*Pteraspis*) *dairydinglensis* sp. nov. and *P.* (*B.*) *crouchi* var. *heightingtonensis* in the middle, whilst arctolepids, notably *Kujdanowiaspis anglica*, become more common in the upper part of the zone. *P.* (*P.*) *dairydinglensis* also occurs at the same level in the Cleobury Mortimer area (Dineley & Gossage, 1959 : 232. . . . a new and distinctive species of *Pteraspis* "), and it is now evident that the specimens from beds 600 to 850 ft. above the base of the Ditton Series recorded as *P. rostrata* (Dineley & Gossage, 1959) are indeed *P.* (*P.*) *dairydinglensis*. *Cephalaspis* fragments occur throughout the zone, which includes near its base the distinctive cephalaspid fauna of Whitbatch (Stensiö, 1932), and also acanthodian and thelodont scales. The diagnostic fauna of the *crouchi* Zone may therefore be regarded as consisting of *P.* (*B.*) *crouchi*, *P.* (*P.*) *rostrata*, *P.* (*P.*) *dairydinglensis*, *Tesseraspis*, ? *Weigeltaspis*, and *Kujdanowiaspis*. This is a much restricted fauna compared with that occurring with *P.* (*B.*) *crouchi* in Herefordshire and Monmouthshire (White, 1950*a* : 56).

As defined above, the arbitrary base of the *crouchi* Zone is here regarded as being 140 ft. above the main " *Psammosteus* " Limestone. The highest horizon yielding *P.* (*B.*) *crouchi* in the type area is about 800 ft. above the main " *Psammosteus* " Limestone, although it has been recorded from a level of 900 ft. in the Cleobury Mortimer area (Dineley & Gossage, 1959 : 232). The lowest horizon yielding a fauna of the succeeding *leachi* Zone, in the Clee Hills, also occurs about 900 ft. above the main " *Psammosteus* " Limestone. This discrepancy between the two areas may be accounted for by the increase in thickness of the Ditton Series, south-eastwards from Brown Clee Hill to Cleobury Mortimer. Thus, the upper limit of the *crouchi* Zone is arbitrarily placed at 850 ft. above the main " *Psammosteus* " Limestone, though it may occur at a somewhat lower level in the north-west of the area and higher in the south-east.

Zone of *Pteraspis* (*Cymripteraspis*) *leachi* White

Like *P.* (*P.*) *rostrata* and *P.* (*B.*) *crouchi*, *P.* (*C.*) *leachi* occurs widely in the Anglo-Welsh area and also on the Continent. In the Clee Hills area it is commonly found in association with *Protaspis* (*Europrotaspis*) *crenulata* sp. nov., and a diversified arctolepid fauna consisting largely of new forms, but including *Kujdanowiaspis anglica*. A rich fauna, with several new genera and species, has been obtained from Besom Farm Quarry (8), but, like many of the upper Dittonian localities to the east of Brown Clee, it is not possible to estimate its height above the main " *Psammosteus* " Limestone. Besom Farm Quarry is also notable for having yielded *Benneviaspis salopiensis* sp. nov., the youngest cephalaspid in this area.

As in the lower zones, acanthodian and thelodont scales form the major part of the micro-fauna, the former persisting to the very top of the zone where they were collected by King, with a fragment of an arctolepid, from a pellety sandstone immediately underlying the lower Abdon Limestone at Walton Quarry (114) estimated to be about 1,450 ft. above the main " *Psammosteus* " Limestone. The highest locality in the area yielding *Pteraspis* is The Thrift (106), some 1,300 ft. above the main " *Psammosteus* " Limestone. In all, the assemblage characteristic of the *leachi* Zone comprises *Pteraspis* (*C.*) *leachi*, *Protaspis* (*Europrotaspis*) *crenulata* sp. nov., *Benneviaspis salopiensis* sp. nov., *Kujdanowiaspis anglica*, *K. willsi* sp. nov., *Wheathillaspis wickhamkingi* gen. et. sp. nov., *Prescottaspis dineleyi* gen. et sp. nov., *Overtonaspis billballi* gen. et sp. nov., *Onchus wheathillensis* sp. nov., *Nodonchus bambusifer* gen. et sp. nov., and *Ischnacanthus* (?) *anglicus* sp. nov.

As shown above, the lowest records of *P.* (*C.*) *leachi* are from about 900 ft. above the main " *Psammosteus* " Limestone (Bockleton Brook and Upper Overton Quarry), but the junction of the *leachi* Zone with the underlying *crouchi* Zone is drawn arbitrarily some 500 ft. below. Upwards, the zone is regarded as extending to the base of the Clee Series, though its upper part appears to be poorly fossiliferous.

(*c*) *Invertebrates*

A varied invertebrate fauna is known from the Lower Old Red Sandstone of the Anglo-Welsh area, but only a few localities yielding invertebrates have been recorded in the Clee Hills district. The occurrence of Mollusca is of particular interest, since they may imply the establishment of brackish water conditions. Lamellibranchs are known from the lowest part of the Downtonian, and *Modiolopsis* sp. occurs just above the main " *Psammosteus* " Limestone at Criddon Bridge (19). The highest horizon yielding lamellibranchs in the Clee Hills is that recorded by the Geological Survey (Eyles, 1953 : 26), about 150 ft. above the " *Psammosteus* " Limestone, near Ditton Priors.

An occurrence of especial interest is the first record of *Spirorbis* from the Old Red Sandstone. A number of specimens were found attached to the interior of the dorsal disc of the holotype of *Protaspis* (*Europrotaspis*) *crenulata* (p. 269 Text-fig. 16; Pl. 43, fig. 3). Like the *Spirorbis* of the *Spirorbis* limestones which occur in the Upper Carboniferous of the Wyre Forest, they imply the establishment of more saline conditions, though lacustrine rather than marine.

Fragments of eurypterids are scattered throughout the lower part of the succession, though they are usually poorly preserved. However, densely packed bands of eurypterid debris incorporating better preserved specimens occur in a green, silty clay at Leath Bank. Crustacean tracks were recorded by Roberts (1863) from a fine sandstone at Bouldon, and further tracks have recently been found there and at Tugford.

(d) *Plants*

Plant remains occur throughout the Downton-Ditton succession, especially the latter, and are usually associated with green, grey or buff shales, siltstones and marly cornstones, and frequently with traces of (?) malachite. A similar association of plant remains with copper minerals was noted by Dixon (1921 : 30, 31) in Pembrokeshire, and he suggested that the precipitation of the malachite may have been effected by the decomposing organic matter, as in the German Kupferschiefer.

The preservation of the plant fragments is almost invariably poor, with the exception of *Pachytheca* which is preserved in both calcareous and carbonized states, and occurs widely throughout the succession. Among the better preserved material, it has been possible to determine *Prototaxites*, *Nematothallus*, ? *Cooksonia*, and *Pachytheca*.

III. UPPER OLD RED SANDSTONE

STRATIGRAPHY

(a) *Farlow Sandstone Series*

The name " Farlow Sandstones " was first applied by King (1925 : 383, 386) to beds outcropping at Farlow and to the south of Titterstone Clee Hill, which contained a typical Upper Old Red Sandstone fauna. However, as has been shown above, the beds outcropping at Clee Burf and ascribed to the Farlow Sandstones (p. 386) are actually Clee Series. King had subsequently arrived at a similar conclusion (*in lit.*), including the beds within his stage III or " Brownstones ". In a later paper King (1934) introduced the term " Farlovian " using it with both a stratigraphical and a time connotation. As Croft (1953 : 430) has pointed out, King subsequently extended it to embrace all Upper Old Red Sandstone beds of the Anglo-Welsh area which unconformably overlie lower horizons. Here, however, it is proposed to retain " Farlovian " purely as a time division and to re-introduce the stratigraphical name " Farlow Sandstones " for the beds of Farlovian age at Farlow and the neighbouring areas.

The total area of outcrop of the Farlow Sandstone Series is very small, the greater part forming the prominent ridge extending east-north-eastwards from Farlow. The remainder consists of small areas outcropping to the south and east of Titterstone Clee Hill.

It has been found convenient to subdivide the Farlow Sandstone Series on the basis of marked lithological contrast into an upper Grey Farlow Sandstone Formation and a lower Yellow Farlow Sandstone Formation.

(i) *Yellow Farlow Sandstone Formation*

As the name implies, the Yellow Farlow Sandstone Formation consists almost entirely of yellow, yellow-buff and sometimes yellow-orange friable sandstones, siltstones and grits. These are largely composed of angular to sub-rounded and sometimes rounded grains of igneous and metamorphic quartz, metamorphic quartzite and quartz-schist, " felsite ", cherts in variety, with rarer grains of muscovite, fresh plagioclase feldspars, tourmaline and garnet (see also Fleet, 1925 : 507). The grain size ranges widely, from silt (0·01 mm.) to grit (3·0 mm.) but averages between 0·02 and 0·8 mm. The grains are poorly cemented, largely by ferruginous and clay cements. Iron staining and thin limonitic banding also occur.

The sandstones tend to be massive and characteristically current-bedded, individual lenses frequently showing rapid alternation of fine and gritty layers which vary widely in degree of sorting. Some of the coarser lenticles are very poorly sorted and it is in these that the most rounded grains commonly occur. The finer sandstones and siltstones are frequently flaggy, with micaceous bedding planes. A few layers of yellow-buff silty marl, rarely exceeding 2 in. in thickness, occur as partings between the sandstone. In contrast, pellets of buff and grey silty marl are commonly incorporated in the sandstones throughout the formation, and also pebbles, largely of vein quartz and to a lesser extent grey and purple quartzites and cherts, especially jasper. The pebbles are mostly sub-angular to angular though a few are rounded, being between 1 and 4 cm. in size. Some of the more conglomeratic lenses also incorporate angular and subangular fragments of sandstone, obviously derived from beds but lately consolidated. The basal 10 ft. of the formation is markedly conglomeratic and contains pebbles up to 14 cm. in size.

The Yellow Farlow Sandstone Formation (which for brevity will hereafter be referred to as the Yellow Formation) is relatively well exposed at Farlow, where its scarp face forms the steep feature of Farlow Bank. An excavation made on the lower slopes of the feature showed the basal conglomerate of the formation to be resting on red-brown silty marls of the Ditton Series. The detailed nature of the contact was obscured by the highly weathered condition of the marls, but there appeared to be little, if any, angular unconformity. The thickness of the Yellow Formation at Farlow is estimated to be about 190 ft., and the dip here, as in the formation along the whole of the Farlow-Walton ridge, averages 20 degrees to the south-south-east.

Eastwards from Farlow, the ridge becomes less steep and exposures are few and poor as far as Oreton, two-thirds of a mile from Farlow, where the Yellow Formation is exposed in a road section along the northern foot of the feature. Although it has not been possible to determine the full thickness of the formation at this point, it appears to be in excess of 110 ft. Still further to the east the feature is much reduced, being breached by the River Rea at Prescott. Here, however, the Yellow Formation again gives rise to a strong feature forming a small river-cliff on the east bank of the Rea, and is well exposed along the road cutting. The thickness of the formation at this point is about 210 ft.

West of Farlow exposures are again few and poor, and the Cornbrook Sandstone oversteps the Carboniferous Limestone and Grey Farlow Sandstone Formation on to the Yellow Formation. However, the Farlow Sandstones again outcrop at Cleeton, 2¼ miles to the south-west.

(ii) *Grey Farlow Sandstone Formation*

The top of the Yellow Formation appears to have been marked by a sudden change in the conditions of deposition, since there is a sharp transition from yellow sandstone and grits to a succession of sandstones, cornstones, rubbly limestone and marls, predominantly grey in colour. The Grey Farlow Sandstone Formation is poorly exposed and such outcrops as occur are mostly of the more resistant sandstones and rubbly limestones. Though the sandstones are largely grey or shades of grey in colour, green, brown, buff and purple bands also occur. Like those of the underlying Yellow Formation they consist predominantly of sub-angular to sub-rounded quartz grains, with grains of quartzite, feldspars and cherts. Similarly, the grain size ranges between silt and grit, but most of the sandstones are fine to medium (i.e. 0·1 to 0·5 mm.).

Many of the sandstones are calcareous, often showing lustre-mottling, and they commonly incorporate small sub-angular and rounded pebbles of vein quartz, cherts, jasper, quartzite and pellets of grey and buff marl. Unlike the homogeneous and relatively massive appearance of the Yellow Formation, the Grey Formation is a far less uniform and more thinly bedded series, individual beds rarely exceeding 4 ft. in thickness. Current bedding is common and many of the finer sandstones are laminated, showing ripple marking and occasionally micaceous bedding planes.

Frequent conglomeratic cornstones occur and are usually grey or green in colour. They are composed largely of fragments of silty and calcareous marl, silty sandstones, and small pebbles like those in the sandstones, set in a matrix of sandy calcareous marl. As in the cornstones of the Lower Old Red Sandstone, fragments of fish are sometimes incorporated.

Also characteristic of the Grey Formation are the lenticular " rubbly " limestone bands, ranging in thickness from a few inches up to 4 ft., which are grey, purple-grey and green-grey in colour. They are composed of fragments of sandy and marly limestone and calcareous sandstone set in a limestone matrix. Sub-rounded, rounded and sub-angular sand grains are commonly incorporated, with occasional pebbles of vein quartz, quartzite and cherts. In thin section, many of the limestones are seen to have a clotted or breccioid structure, having undergone a varying degree of recrystallization, with large zones or centres of finely-crystalline calcite set in a coarsely crystalline matrix. Like the conglomeratic facies of the Abdon Limestones it seems probable that the limestone originated from the breaking up of sheets and crusts of muddy and sandy limestones, with pene-contemporaneous re-cementation by muddy limestones. In several instances secondary precipitation has occurred around many of the fragments. The rubbly limestones are frequently associated with white lustre-mottled sandstones, a further parallel with the Abdon Limestones.

Though the marl pellets which form such a conspicuous element in the composition of the cornstones and many of the sandstones are mainly grey and shades of grey in colour, most of the marls seen to outcrop are red with subordinate green bands. A well-marked red marl, some 6 ft. thick, outcrops immediately above the Yellow Formation, forming the basal member of the Grey Formation. However, owing to the lack of exposures it has not proved possible to assess the total proportion of marls present in the latter.

To the south of Prescott the Grey Formation is estimated to be 275 to 300 ft. thick and is overlain by the basal conglomerate of the Carboniferous Limestone. At Oreton the thickness is reduced to 100 ft., and at Farlow only 40 ft. is present. The significance of this great thinning of the Grey Formation is reflected in the topography and will be discussed below. At Prescott, the Farlow Sandstone Series gives rise to two well-marked escarpments, one formed by the Yellow Formation and the other by the upper part of the Grey Formation, capped by the basal conglomerate of the Carboniferous. Owing to the thinning of the Grey Formation these merge to form a single feature at Oreton, which continues westwards to Farlow.

FAUNA

Though poorly fossiliferous, the Farlow Sandstone Series has long been known to contain a characteristic Upper Old Red Sandstone fish fauna (Egerton, 1862 : 103–105 ; Traquair, 1894–1906 : 128, 129). That collected from the Yellow Formation is largely fragmentary, with a few rare complete plates and scales. With the exception of the original finds described by Egerton, all are in the form of moulds, and despite the fact that most are preserved in medium to coarse, and even gritty sandstones, the detail of the ornamentation is mostly good. In some instances the vascular cavities have been preserved as a delicate filigree of limonitic mud. Apart from the classic locality at Farlow, the exact position of which is now unknown, only two new localities in the Yellow Formation have yielded fossils, one at Farlow (29), the other at Prescott (82). The latter has proved to be the more prolific, the fragments being concentrated in a small lens of gritty sandstone, obviously representing a winnowed deposit. But here, as at Farlow, other plates occur scattered randomly in finer sandstones. Forms represented include *Bothriolepis* sp., *B. macrocephala*, *Holoptychius* sp., *Pseudosauripterus anglicus* gen. nov., *Eusthenopteron farloviensis* sp. nov., and indeterminate crossopterygian and dipnoan remains.

The Grey Formation is even less fossiliferous than the underlying Yellow Formation, having yielded only a small fauna of mostly indeterminable bone fragments, but including *Holoptychius* sp. The fragments come from the stream section at, 710 yds. (112) and 800 yds. (113) south-south-east of Prescott, in grey, calcareous pebbly sandstones and cornstones, and are much abraded.

IV. LOWER CARBONIFEROUS

(a) *Basal Conglomerate*

Though seemingly outside the scope of the present paper, a brief account of the conglomerate which occurs between the base of the Carboniferous Limestone and the top of the Grey Farlow Sandstone Formation forms a necessary corollary to a description of the latter. The conglomerate has been variously regarded as constituting the uppermost part of the Upper Old Red Sandstone ; as forming the basal bed of the Carboniferous ; and as a transitional bed between the two.

The conglomerate is buff-brown and orange in colour and is largely composed of angular and sub-angular quartz grains, ranging in size between 0·1 and 3·0 mm., the coarser grades predominating. It is as a whole friable, being poorly cemented by ferruginous and calcareous cements. Current bedding is characteristic and the lenses of fine-grade material are usually better cemented. The constituent pebbles range upwards from 0·3 to 15 cm. in size and are mostly sub-angular to sub-rounded. By far the greater proportion are of white and pink vein quartz, with numerous pebbles of purple, pink, yellow and grey quartzites, cherts in variety, jasper and " lydite ".

The conglomerate forms a prominent crest along the greater part of the Farlow-Walton ridge, and is exposed at several points. In the road section of Farlow Bank it is some 6 ft. thick, but owing to slipping its relationship with the underlying Grey Farlow Sandstones and the overlying Carboniferous Limestone is not clear. Eastwards from Farlow, the conglomerate begins to increase in thickness, being some 12 ft. thick at " The Rough ", one-third of a mile due east of Farlow Church. Here, the top of the conglomerate becomes progressively more calcareous upwards, passing into thin-bedded, sandy, pebbly limestones containing numerous crinoid ossicles and characteristic Carboniferous Limestone brachiopods, which are succeeded by typical limestone shales. The conglomerate is not well exposed at Oreton but appears to be at least 12 ft. thick.

The greatest development of the conglomerate is at Prescott, where it is some 35 to 40 ft. thick and gives rise to a small but well-marked escarpment. But neither here nor elsewhere is there a reliable exposure of the contact of the base of the conglomerate with Grey Farlow Sandstones. However, since as will be shown below, the conglomerate truncates the Grey Farlow Sandstone Formation, and in view of the passage from it into the Carboniferous Limestone, the conglomerate can be regarded as forming the basal bed of the Carboniferous. The limestone shales into which the conglomerate passes upwards have been assigned by Vaughan (1905 : 252–254) to his *Cleistopora* zone. Thus the conglomerate may well represent the lower part of K.

V. STRUCTURE

(a) *Folding*

The principal tectonic feature of the area is the folding of the strata along Caledonoid axes to form three major, asymmetrical but relatively simple structural units, the Brown Clee and Titterstone Clee Synclines and the interposing Ledwyche Anticline.

Brown Clee Syncline. The north-western margin of the Brown Clee Syncline is delimited by the Church Stretton fault zone. Its broad north-western flank comprises Ordovician strata dipping south-eastwards from the Stretton Hills, succeeded by the Silurian in Apedale, Wenlock Edge and Hopedale, and in Corvedale by the Downton and Ditton Series dipping at 5 to 10 degrees. The south-eastern flank of the syncline is, in contrast, very narrow and the strata are in general more steeply inclined ; whilst its core is formed by the Clee Series of Brown Clee Hill. The axis of the syncline extends east-north-eastwards from Bromfield, to Hopton Cangeford ; there it swings north-eastwards to Warren Cottage, near which it can be accurately determined in a stream section, and thence to Clee Burf, up to which point it plunges steadily to the north-east. Between Clee Burf and Cleobury North Liberty the direction of plunge becomes reversed and the axis extends east-north-eastwards nearer to the topographic axis of the hill, and it is also paralleled by the plane of the Brown Clee Fault. From Cleobury North Liberty the axis reverts to a north-easterly direction, extending through Morville to Linley and plunging to the south-west.

Titterstone Clee Syncline. This has previously been referred to as the " Clee Hill Syncline " (Whitehead & Pocock, 1947 : 120), but to avoid possible confusion it is here specifically related to Titterstone Clee Hill. It is a more complex structure than the Brown Clee Syncline since in the area of Titterstone Clee Hill it incorporates several subsidiary, but well-defined folds. However, only the north-eastern extremity of the syncline occurs in the area being described and here the subsidiary folding is not evident. Like the Brown Clee Syncline, the Titterstone Clee Syncline is asymmetrical, with a broad north-western flank dipping at 10 to 20 degrees to the south-east, increasing towards the Farlow-Walton ridge where dips of up to 65 degrees occur in the Avonian Limestones. It is possible that these latter dips are, at least in part, a consequence of the collapse and slipping of the limestones into the subterranean stream course which drains from Farlow eastwards to the Factory Cottages, along the southern margin of the ridge (Morris & Roberts, 1862 : 96). The few dips which have been obtained from the succeeding Cornbrook Sandstone indicate that they are inclined at a very much shallower angle, averaging 10 degrees. The south-eastern flank of the syncline is narrow and in the present area consists of Ditton Series dipping moderately steeply, averaging 30 to 40 degrees, to the north-west. The axis of the Titterstone Clee Syncline is difficult to determine with accuracy owing to the cover of the Cornbrook Sandstone and the Coal Measures, but in general it diverges slightly from that of the Brown Clee Syncline, extending from Knowbury east-north-eastwards to Catherton Marshes where it swings to the north-east, continues to Bagginswood, and becomes coincident with the Titterstone Clee Fault.

Ledwyche Anticline. This is an asymmetrical structure separating the Brown Clee and Titterstone Clee Synclines, the north-western flank being narrow and more steeply inclined than the broader south-eastern flank. Its axis is broadly parallel to that of the Brown Clee Syncline and extends east-north-eastwards from Middleton to Langley, and then north-north-eastwards to Coldgreen, where it swings round to assume a north-eastwards course to Underton. In the area of Coldgreen there is some evidence that the fold axis is associated with local faulting. The axis of the Ledwyche Anticline plunges steadily to the north-east, though the amount of plunge decreases between Langley and Underton, north of which it appears to die out.

To the south-west the Brown Clee and Titterstone Clee Synclines, with the interposing Ledwyche Anticline, merge into the structural complex of Silurian strata extending between Ludlow and Presteign and delimited on the west by the Church Stretton fault zone. The relatively more complex structure of the Titterstone Clee Syncline is reflected in its south-westward prolongation through Caynham into the more tightly folded area extending from Richard's Castle, through Leinthall Earls to Presteign, accompanied by a well-defined fault-belt. It has also been suggested that the Titterstone Clee Syncline itself forms the south-western prolongation of the Stafford Syncline (Whitehead & Pocock, 1947 : 122). The Ledwyche Anticline expands south-westwards into the broad anticlinal core in Wenlock Shales at Wigmore Rolls, whilst the Brown Clee Syncline noses out in the area of Adforton. However, to the south-west of the Silurian structural complex extending from Ludlow to Kington, the broad fold of the Brown Clee Syncline appears to have a southern counterpart in the Mynydd Eppynt. To the north-east of the present area the folds become much reduced and lost beneath the Coal Measures of the Wyre Forest.

(b) *Faulting*

There is considerable evidence of faulting in the area, but except where such well-defined horizons as the " *Psammosteus* ", Abdon and Avonian Limestones are affected, the extent, direction and downthrow of the faults are difficult to determine. The majority of the faults are orientated broadly NE.–SW., parallel to the main fold axes, with a minor series approximately at right angles to them. In the few instances where the hade and throw can be determined, the faults appear to be normal. The area is affected by two major faults, the Brown Clee Fault and the Titterstone Clee Fault, both associated with the two major fold axes.

Brown Clee Fault. Nowhere has the plane of the Brown Clee Fault been seen to outcrop, but its effects can first be traced near Gibbridge in the Ledwyche Valley, where it has a Caledonoid trend and downthrows the main " *Psammosteus* " Limestone some 150 ft. to the south-east. North of Gibbridge the fault appears to follow a gently sinuous but broadly N.–S. course, faulting out a prominent sandstone/cornstone feature at Bank House, and downthrowing the Abdon Limestones some 200 ft. to the east near Bockleton Court, where the fault begins to swing round again to the north-east. The Coal Measures of Brown Clee Hill are poorly exposed and it is difficult to trace the fault across them, but it upthrows a narrow strip of Coal Measures to the north-west of Clee Burf, and downthrows the south-eastern portion of the Abdon Burf outcrop. At Hillside, the Brown Clee Fault again displaces the Abdon Limestones, though to a lesser degree than at Bockleton Court, namely some 75 ft. to the east. Over the southern part of Brown Clee Hill the course of the fault appears generally to coincide with the axis of the Brown Clee Syncline. The effects of the fault can next be detected in the stream section 400 yds. south-east of Middleton Priors, and again at Moore Dingle, three-quarters of a mile south-west of Aston Eyre, where the " *Psammosteus* " Limestones are downthrown some 150 ft. to the east.

Titterstone Clee Fault. The present area includes only the north-eastern part of the Titterstone Clee Fault, which extends north-eastwards from Hope Bagot on the southern slopes of Titterstone Clee Hill, in which area it displaces the outcrop of the Avonian Limestones between Gorstly Rough and the Novers, and throws Coal Measures against Lower Old Red Sandstone to the south and south-west of Clee Hill. At Catherton Common the Cornbrook Sandstone is thrown against both Downtonian and Dittonian strata, and though it has not proved possible to measure the amount of downthrow, it would appear to be at least 1,000 ft. to the north-west. North-eastwards from Catherton Marshes the line of the fault coincides broadly with the axis of the Titterstone Clee Syncline, and is defined to the east of the River Rea by vertical and disturbed strata in exposures half a mile north of Detton Hall. Here the fault appears to bifurcate, the main branch extending north-north-eastwards between Prescott and Walton, throwing the Farlow Sandstone Series against the Clee Series, and continuing as the Deuxhill Fault (Whitehead & Pocock, 1947 : 131). The subsidiary branch extends at first east-south-eastwards and can be traced in the stream section to the south of Walton where the beds are contorted and disturbed ; it then gradually swings northwards through Bagginswood, where it is possibly joined by the Brock Hall or Billingsley Fault (Whitehead & Pocock, 1947 : 130). From Bagginswood it continues north-north-eastwards to rejoin the main branch south-west of Chorley. It seems probable that the Titterstone Clee Fault links up to the south-west with the fault extending between Caynham Camp and Leinthall Earls.

Faulting exerts considerable influence on the Farlow-Walton Ridge which, as noted by Murchison (1839 : 121), is broken by a series of dip-faults into a number of blocks which are slightly displaced relative to each other. The amount of downthrow appears to be small, not exceeding 100 ft., and is in most instances to the west. It is along the line of one of the faults that the River Rea cuts across the ridge at Prescott. The escarpment of the "*Psammosteus*" Limestones also shows a number of small displacements owing to minor faulting, as do the Abdon Limestones at Abdon Liberty and Nordybank, again the amount of downthrow usually not exceeding 100 ft.

(c) *Unconformities*

The sequence from the Upper Ludlow Series to the top of the Clee Series is perfectly conformable and there is no evidence to support the existence of the unconformity postulated by King (1934 : 529 ; *in lit.* ; see also Wills, 1948 : 29, 30) to occur at the base of his "Brownstones" or "Division III". It is evident from King's field-maps (deposited in the Department of Geology, University of Birmingham) that on the western side of Brown Clee Hill his "Brownstones" are broadly equivalent to the Clee Series of the present classification. However, to the east of the hill, King includes a large area of what can now be shown to be the Ditton Series within his "Brownstones". In postulating an intra-Lower Old Red Sandstone unconformity, King was obviously influenced by the alleged unconformity claimed by Miss D. M. Williams (1926 : 219–225) to occur beneath the Brownstones in the Gower area. But this too has been disproved (George, 1939 : 1–5 ; Croft, 1953 : 429), there being an unbroken sequence from Downtonian to Breconian in South Wales as in the Welsh Borderland.

As is proved by their faunas, a large time-gap exists between the Farlow Sandstone Series and the underlying Lower Old Red Sandstone, yet the angular disconformity between them appears to be very slight. At Farlow the Farlow Sandstones rest upon high Ditton Series, but owing to a divergence in strike, the Dittonian striking NE.–SW. and the Farlovian a little south of east, the Farlow Sandstones rest upon successively higher beds eastwards to Prescott. Between Prescott and Walton it is probable that the Farlow Sandstones overstep onto the Clee Series though the junction is buried beneath the Farlovian cover, the latter having been eroded from the upthrown wedge of Clee Series at Walton. King (1925 : 386) states that beds which he regards as being Farlow Sandstones show much greater angular disconformity on the southern Flanks of Titterstone Clee Hill, where they rest across denuded fold axes in Downtonian and Dittonian strata.

A further break occurs at the top of the Farlow Sandstone Series, although these have previously been suggested to have a perfectly conformable relationship with the succeeding Carboniferous Limestone (King, 1925 : 389 ; Dixon, *in* Watts, 1925 : 395). Again, it is difficult to detect any angular disconformity between the two series except at Farlow, where it may be more apparent than real owing to slipping. However, the magnitude of the break is demonstrated by the relationship of the basal Carboniferous Conglomerate to the underlying Grey Farlow Sandstone Formation. South of Prescott the conglomerate rests upon 275 to 300 ft. of the Grey Farlovian ; three-quarters of a mile to the west at Oreton the Grey Farlovian has become reduced to 100 ft., whilst at Farlow a further three-quarters of a mile to the west it is only 40 ft. thick. Owing to lack of exposures it has not proved possible to ascertain whether the basal conglomerate oversteps onto the underlying Yellow Farlovian to the south-west of Farlow, but south of Silvington an attentuated Avonian sequence and the Grey Farlovian (if present) are overstepped by the Cornbrook Sandstone.

The relationship of the Cornbrook Sandstone to the underlying strata between Cleeton and Factory Cottages, and also on the western flanks of Titterstone Clee Hill, has led one of the writers (H. W. B.) to arrive independently at the same conclusions as George (1956 : 308, 309) regarding its unconformable nature. The Cornbrook Sandstone is itself unconformably overlain by Coal Measures which can be correlated with the Kinlet Beds (Ammanian) of the Wyre Forest Coalfield. The latter beds rest upon Ditton Series along the south-eastern margin of the area and in small outliers near Middleton Scriven and Chorley, whilst the Coal Measures of Brown Clee Hill which are of the same age (Whitehead & Pocock, 1947 : 45–47) rest upon Clee Series. As has been pointed out by Whitehead & Pocock (1947 : 44), in each of these areas, as at Titterstone Clee, the base of the Coal Measures is marked by a distinctive white or grey, hard sandstone which may in part be conglomeratic. A further unconformity occurs between the Kinlet Beds and the succeeding Highley Beds (Morganian) which overstep onto the Ditton and Downton Series in the north-east of the area.

(d) *Age of the Movements*

The principal folding movements affecting the area were those of the Caledonian orogeny which uplifted the Lower Old Red Sandstone of the whole of the Anglo-Welsh region. These movements were of post-Breconian, pre-Farlovian date, but since the upper limit of the age of the Breconian is unknown, though it may extend into the Middle Old Red Sandstone (Croft, 1953 : 431), more precise dating with reference to the continental Devonian stages is impossible. Jones (1956 : 334) has shown that much faulting accompanied the Caledonian folding in South Wales, but it has not proved possible to distinguish any undoubted Caledonian faulting in the Clee Hills, though the alignment of the major faults with the folds indicates some degree of interrelationship. This is particularly apparent in the association of the Brown Clee and Titterstone Clee Synclines and Faults, and in the former instance there is some indication that the Coal Measures are less affected by the Brown Clee Fault than the underlying Clee Series. However, even this can only be taken as evidence of pre-Kinlet Beds faulting with subsequent post-Kinlet Beds rejuvenation. Whatever the age of the faulting, since it appears to be normal, it occurred during periods of tension interspersed between phases of major compression.

A characteristic feature of the folds, and also of the Neen Savage Anticline and the Cleobury Mortimer Syncline to the south (Dineley & Gossage, 1959 : 233), is their asymmetry ; the synclines having broad, north-western flanks and narrow, more-steeply dipping, south-eastern flanks, the anticlines showing the reverse. It has not been possible to determine whether this is an original feature of the Caledonian folding movements, but even if this was so the asymmetry was further accentuated by Carboniferous movements (see also Squirrell & Tucker, 1960 : 167–170). This is demonstrated by the Cornbrook Sandstone which in the area of Cleeton on the north-western flank of the Titterstone Clee Syncline dips at about 10 degrees to the south-east, whilst near to Clee Hill, on the southern flank, it dips to the north-west at 60 to 70 degrees. A further feature of the folds is the gradual swing in strike from the Armoricanoid trend of the Cleobury Mortimer Syncline (Squirrell & Tucker, 1960) to the typical Caledonoid direction of the Brown Clee Syncline, the folds seemingly having rotated about Titterstone Clee Hill. Moreover, due north of the hill the axes of the Ledwyche Anticline and the Brown Clee Syncline have been deflected northwards, as has the Brown Clee Fault ; whilst along the same line the dolerite intrusions of both Brown Clee and Titterstone Clee occur. It is probable that all these features, plus the more complex form of the Titterstone Clee Syncline itself, are reflections of the influence of pre-Caledonian structures at depth.

The Caledonian orogeny was succeeded by a period of epeirogenic movements, marked by unconformities between the Farlow Sandstone Series and the Carboniferous Limestone, and between the latter and the Cornbrook Sandstone. A more profound phase of movement involving some degree of folding followed the deposition of the Cornbrook Sandstone which George (1956 : 307–309) has suggested to be most probably of Namurian age, and preceding the " Middle " Coal Measures or Ammanian (= " Yorkian ". Whitehead & Pocock, 1947 : 40). This was succeeded by early Morganian (= " Staffordian ". Whitehead & Pocock, 1947 : 121) movements, regarded by Wills (1956 : 59) as representing the First Malvernian Movements, and evidenced by the marked overstep of the Kinlet Beds (Ammanian) by the Highley Beds (Morganian) onto the Downton and Ditton Series in the north-east of the area. The only direct evidence of post-Morganian movement in the area is provided by the Deuxhill Fault which throws Highley Beds against Lower Old Red Sandstone ; and it has been suggested (Whitehead & Pocock, 1947 : 122) that the Titterstone Clee Syncline, and presumably the Brown Clee Syncline, owe their present elevation to post-Triassic movements. However, as is shown by the configuration of the Coal Measure basins of Brown Clee and Titterstone Clee, post-Caledonian movements continued folding and faulting along pre-existing axes.

VI. CONDITIONS OF DEPOSITION AND PALAEOGEOGRAPHY

It is necessary to consider the history of the Clee Hills area in the broader context of that of the Anglo-Welsh region. The major tectonic units of the Anglo-Welsh region as defined by Wills (1951) comprise the Welsh geosyncline (Jones, 1938) and the Midland kratogenic block, the boundary between the two broadly delimited by the great line of disturbance extending from Pembrokeshire, through Church Stretton, and possibly northwards into the Lake District (Jones, 1927). By the end of Silurian times the rate of subsidence in the geosyncline had begun to slow down, and the presence of layers of phosphatic pebbles or " bone-beds " in the sediments of the marginal zones indicates pauses in subsidence, or even periods of emergence of areas of the Midland block above the shallow shelf sea which covered it (Lawson, 1954, 1955 ; Squirrell & Tucker, 1960).

The base of the Old Red Sandstone is marked by the Ludlow Bone Bed (White, 1950*a* : 63), a remarkable deposit which has been recorded from a number of localities ranging over a wide area of the Welsh Borderland, and also South Wales (Walmsley, 1959) and the Midlands (King & Lewis, 1912 ; Whitehead & Pocock, 1948 ; Ball, 1951). It appears to be a remanié deposit (Whittard, 1952 : 176, 177) resulting from a prolonged pause in subsidence over the whole area, which marks the inception of the main phase of the Caledonian orogeny, and was accompanied by folding in South Wales. Although the actual bone-beds are lenticular, the Ludlow Bone Bed forms a stratigraphical unit which is probably broadly synchronous over the whole of the area (cf. Denison, 1956 : 389). The conditions of deposition of the Ludlow Bone Bed indicate shallow waters with active bottom currents, and alternation of marine and brackish environments (see Wills, 1948 : 25 ; Whittard, 1952 ; Denison, 1956). Other thin, lenticular bone-beds occur in the lower part of the overlying Grey Downton Formation.

In the Ludlow area, the Ludlow Bone Bed is succeeded by the Downton Castle Sandstone which marks the inception of the great delta plain which formed the major palaeogeographic feature of the Lower Old Red Sandstone. The Downton Castle Sandstone comprises thick, current-bedded sandstones interbedded with laminated siltstone and shales. Despite the evidence adduced by Denison (1956 : 390, 391) for the marine origin of the Downton Castle Sandstone, the lithology, fauna and flora of the sandstones are strongly indicative of fresh-water or brackish deltaic conditions ; whilst the siltstones and shales are brackish, with rare marine incursions. Similar conditions obtain in the South Staffordshire area (Ball, 1951), where there is no need to postulate a lateral facies change to account for the presence of *Hemicyclaspis murchisoni*, as suggested by Schmidt (1959 : 28). But in the geosynclinal zone to the west of Ludlow (Stamp, 1919 ; Earp, 1938, 1940 ; Holland, 1959) the equivalent beds are finer grained, and much more brackish in character, with marine bands near the base and they are considerably thicker. Thus it appears that the sandy-delta facies were confined to the north-western area of the Midland block, whilst the very late stages of geosynclinal subsidence were continuing in the Kerry-Knighton areas, where a brackish-water lagoon environment obtained. The sediments would therefore possibly have been derived from areas lying to the north and possibly the east. Thus the Grey Downton Formation thins north-eastwards from Ludlow (p. 182), and in South Staffordshire the sedimentary structures in the equivalent of the Downton Castle Sandstone indicate a north-easterly origin (Ball, 1951 : 232). The presence of thin, highly localized bone-bed lenticles in the lower part of the succession throughout the area, suggests further brief pauses in subsidence.

In the upper part of the Grey Downton Formation the conditions were largely brackish-water lagoonal, with rare marine incursions, though plant fragments occur disseminated throughout the shales. However, the transition from predominantly grey to red sediments which takes place at the top of the Grey Downton Formation, marks a profound change in the geographic and climatic conditions. Some of the views regarding the conditions under which the Old Red Sandstone was deposited have been summarized by Jones (1956 : 336–338) and, as he points out, many of the early opinions favoured an arid climate. However, many of the Downtonian and

Dittonian marls are strikingly similar to the superficial deposits accumulating at present in parts of Africa with a tropical monsoonal climate. Indeed, red and green colours in sediments are no longer regarded as indicating deposition under arid conditions, but rather of intense weathering under hot, humid conditions (Krynine, 1949). Thus, the dominant red coloration of the Downton and Ditton Series, as well as their lithology, implies a profound alteration in the climatic conditions prevailing over the land-mass from which they were derived.

In the Downton Series marls predominate and suggest an ample supply of lateritic clays resulting from tropical weathering, and deposition under quiet conditions. The marls are probably fluviatile, many being highly micaceous, though some of the clay and silt particles may have been wind-borne. The " race " and nodular limestones appear to be penecontemporaneous with the marls, and may have originated like the Kunkar deposits of modern tropical deltas. There is ample evidence of the fluviatile origin of the pellet rocks and of the sandstone bands and lenses, many of which occur in channels cut into the underlying beds. Current ripple-marks are common, and to a lesser extent desiccation-cracks and rain-prints. The pellet beds probably originated from the erosion of sun-baked clay crusts by " flash " floods, with rapid disintegration of the crusts, attrition of the fragments and re-deposition. Brackish and brackish-marine incursions are marked by bands containing *Lingula* and molluscs, whilst a trilobite has been recorded from the lower part of the Red Downton Series at Ledbury (Piper, 1898). In the upper part of the succession sandstones become more common, e.g. the Holdgate Sandstones, as well as cornstones incorporating fragments of fish. The amount of plant debris also increases, whilst bands with invertebrate fossils are rare.

The overall impression is one of a broad delta-plain, similar to the sub-aerial part of the present Colorado delta (Sykes, 1935). This covers an area of some 3,250 square miles, and all but the finest material is deposited by braided and shifting streams, periodically flushed into coalescing flood sheets. Sediment is then rapidly deposited over wide areas, and the mud plains and flats are left dotted with playas and ox-bow lakes. Elsewhere, mud banks and old levées are eroded and current-raked. Reworking of the sediments is common, and deposition takes place not only in stream channels but occasionally over wide continuous areas. Plant debris is accumulated and macerated by the floods, and is often thinly spread over the flats. Though deposition is very near to sea level, sedimentation is active enough to prevent the advance of the sea over the delta, except in rare incursions (cf. Denison, 1956 : 392, 393).

At its maximum during the Downtonian and Dittonian, the delta probably extended over the greater part of South and Central Wales, its western limits being formed by the uprising Caledonian Mountains, and across the Midland kratogenic block at least as far as North London, its southern margin being formed by the great geosyncline extending from Southern Ireland, through the Bristol Channel, into France and Germany (Simpson, 1951 : 60, 61).

Owing to the lack of fossils in the Old Red Sandstone outcrops to the west of the Church Stretton fault zone, it is impossible to correlate them with the sequence in the type area. Moreover, the " *Psammosteus* " Limestones have not been detected west of the Clee Hills area. However, in the Knighton district, Holland (1959 : 472) gives a thickness of approximately 2,000 ft. for his " Red Downtonian ", which consists of red and green " marls " and sandstone bands. He also points out that cornstones, typical of the Dittonian, are absent, implying a correlation wholly with the Red Downton Formation of the Clee Hills. In the Clun Forest area, Earp (1938 : 127) records a thickness of 1,000 ft.+ for his " Red Downtonian Beds ", but again, it is impossible to correlate them with the type sequence. If these western outcrops are of Downtonian age, the thickness of 2,000 ft. in the Knighton area, compared with 1,200 ft. in the Clee Hills, implies that the rate of subsidence and sedimentation continued to be greater in the basin to the west of the Church Stretton fault zone than on the kratogenic block to the east.

The " *Psammosteus* " Limestones, which extend over the greater part of the Anglo-Welsh Old Red Sandstone outcrop from Shropshire to Pembrokeshire, mark a widespread change in the conditions obtaining over the delta, probably effected by slight variations in geography and climate. The limestones probably originated in a series of lagoons with restricted circulation, and though the " *Psammosteus* " Limestones " phase " was of short duration, it appears to have been broadly synchronous over the whole of the area. As has been shown above, the " *Psammosteus* " Limestones have not yet been found west of the Church Stretton fault zone, and there is no information regarding their extent to the east of its present outcrop. However, during a re-examination of the Streatham Common Boring (Whitaker 1889 : 224–229) instigated by Mr. J. D. D. Smith of the Geological Survey,[1] fragments of fish from the core at a depth of about 1,225 ft. were examined by Mr. H. A. Toombs and determined as *Traquairaspis symondsi*, *Tesseraspis tessellata* and (?) *Corvaspis*. These forms indicate a high Downton or low Ditton horizon, but broadly about the level of the " *Psammosteus* " Limestones. The presence at this level of beds of typical Old Red Sandstone facies in South London raises the interesting point of their relationship with the vertebrate-bearing marine strata of " . . . a late Downtonian or post-Downtonian . . . " age (Straw, 1933 : 139), occurring in the Little Missenden Boring, some 30 miles to the north-west.

The " *Psammosteus* " Limestones usher in a change of conditions between the Downton and Ditton Series ; the sediments become coarser and thick cornstone lenses are developed. Fluviatile conditions are well established, with marked lenticularity of the beds, current bedding, ripple-marks, desiccation-cracks and washouts. These changes probably reflect an increase in the tempo of the uplift of the Caledonian mountains with attendant increase in gradient and rainfall. Associated with this, fish and plant remains become more abundant, particularly in the lower part of the Ditton Series. Erosion surfaces are common, some being deeply incised, suggesting intermittent " sheet " or " flash " flooding, with swiftly flowing but heavily laden streams, which were braided and shifting. Sudden floods flushing out the streams of a hilly region and debouching onto the delta would doubtless engulf living fish, as well as dead organisms and plant debris. The cornstones of the Ditton Series, which are the richest source of fossils, are formed by the pene-contemporaneous erosion of layers of muddy limestone and calcareous mud resulting from such floods. The pellets may be well consolidated or plastic, and vary from angular to rounded, the fish remains being incorporated as fragments. The cornstones are markedly lenticular and frequently well sorted. Nodular limestones and " race " similar to those of the Downton Series also occur. The presence of rare bands of lamellibranchs in the lower part of the Series and *Spirorbis* in the upper indicates brief periods of increased salinity, though in the case of the latter implying playa lacustrine, rather than marine conditions. The Ditton Series are not known to outcrop west of the Church Stretton fault zone, but an extrapolation of their thickness from the Clee Hills implies their continuity into Central Wales. However, it is not possible to determine whether sedimentation continued to be greater in the geosynclinal region or on the margin of the kratogenic block.

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[1] The authors are indebted to the Director of the Geological Survey for permission to publish this information.

Towards the end of Lower Dittonian times there appears to have been a slowing down in the uplift of the Caledonian mountains which is reflected in the sediments becoming finer, with silts greatly predominating over sandstones and cornstones. Thereafter, the increasing coarseness of the strata, persisting into the uppermost Clee Series, reflects renewed and accelerated uplift of the mountains culminating in the main phase of the Caledonian orogeny. In the area of the Clee Hills, the end of the Dittonian is marked by the re-establishment of conditions similar to those under which the " *Psammosteus* " Limestones originated, with the formation of the lower of the Abdon Limestones. A further period of normal conditions ensued before the recurrence of the calcareous lagoon environment and the deposition of the upper Abdon Limestone. The appearance and structure of some of the limestones in the Clee Series suggests that they may have been formed in a manner similar to recent surface limestones, or " calcrete " (see Du Toit, 1954 : 445–447).

The coarse sandstones and grits of the Clee Series with predominantly sub-angular pebbles, imply increased gradients and the closer proximity of mountain footslopes. The composition of the sandstones indicates that an area of metamorphic and igneous rocks was being subjected to erosion, though some of the pebbles of quartzite and jasper may have been secondarily derived. The source of the Upper Silurian limestone pebbles in the Clee Series poses a problem. It seems likely that the nearby Silurian outcrops of the Welsh Borderland and West Midlands were blanketed by a thick cover of Downtonian and Dittonian rocks by the beginning of Breconian times. However, the pebbles may have been derived from outcrops which lay to the north-east. The Breconian delta probably extended over the whole of the Anglo-Welsh area, though its eastern limits are unknown. It is not possible to estimate the original thickness of the Clee Series, but it may well have compared with that of the Breconian strata in the Brecon Beacons, namely 2,100 ft.+ (Croft, 1953 : 429).

Between Breconian and Farlovian times the Anglo-Welsh Caledonian orogeny reached its culmination and was succeeded by a period of profound erosion and planation, the whole of the Breconian and the upper part of the Dittonian strata having been removed from the area between Brown Clee Hill and Walton prior to the deposition of the Farlow Sandstones. The Yellow Farlow Sandstones appear to mark the re-establishment of deltaic conditions, with ample evidence of very vigorous stream action. The climate appears to have been relatively arid, but a sudden change in climatic conditions ushered in the deposition of the Grey Farlow Sandstones, with a return to monsoonal conditions similar to those of the Dittonian, and with broadly similar types of sediments. In the Clee Hills area the Farlovian strata appears to be wholly fluviatile with an extremely sparse freshwater fish fauna, and in the Grey Farlow Sandstones a few carbonaceous plant remains. The Farlovian delta extended over a wide area, Farlovian strata outcrop in the Forest of Dean, Bristol and the Mendips, and are well represented in South Wales where in the upper part of the succession they interdigitate with marine Devonian beds. Moreover, Farlovian deposits are known from boreholes in the North and East Midlands, as well as the North London area where they are overlain by marine Devonian. Thus the Midland block persisted as an area of relative stability undergoing subsidence, its southern margin being delimited by approximately the same line as that of the Dittonian, extending from Southern Ireland, through the Bristol Channel and the London area, into France. Its northern extent is equivocal but may have persisted into North England (Wills, 1951 : pls. 3–5).

In the area of the Clee Hills, the Upper Old Red Sandstone was terminated by a period of uplift, erosion and planation prior to the deposition of the basal Carboniferous conglomerate and the advance of the sea.

VII. LIST OF LOCALITIES, FAUNA AND FLORA

In addition to the authors' localities, this list incorporates what may be termed " classic " localities and many fossiliferous horizons discovered by the late W. W. King. Where no faunal list is given, the material requires further preparation.

The national grid reference and 2½ inch new series O.S. sheet number are given for each locality, though in the old series the prefix " SO " is replaced by " 32 ", i.e. SO/68 new series = 32/68 old series. Wherever possible the position of each locality is given relative to the main " *Psammosteus* " Limestone, for which the abbreviation " *P* ". L. is used throughout.

1. ABDON BRIDGE SO/58
1,050 yds. E. 6° S. of Tugford Church (5668/8696).
Cornstone outcropping in bank of stream.
Ditton Series, lower group ; *c.* 140 ft. above " *P* ". L.
Tesseraspis sp.

2. ASTON HILL WOOD 1 SO/69
500 yds. W. 42° S. of Morville Church (6663/9358).
Loose blocks in field below wood, not *in situ.*
Stratigraphical position uncertain.
Pteraspis (*Simopteraspis*) *leathensis* White.

3. ASTON HILL WOOD 2 SO/69
430 yds. S. 28° W. of Morville Church (6679/9355).
Red cornstone exposed in bank.
Stratigraphical position uncertain.
Pteraspis sp.
Poraspis sp.

4. Bache Mill SO/58
170 yds. W. 39° N. of Bache Chapel (5013/8614).
Ludlow Bone Bed.

5. Batch Brook SO/68
1,530 yds. S. 6° E. of Wheathill Church (6232/8076).
Cornstone outcropping in southern bank of stream, a little distance below new footbridge.
Ditton Series, lower group ; *c.* 800 ft. above " *P* ". L.
Pteraspis (*Belgicaspis*) *crouchi* var. *heightingtonensis* White.
Arthrodire.
Thelodont scales.
Acanthodian scales.

6. Baucott, Sandy Lane SO/58
510 yds. N. 31° W. of Broncroft (5430/8710).
Green and red sandstones in old quarry on north side of lane.
Downton Series, Red Downton Formation.
Indet. spine.

7. Beaconhill Brook I SO/69
1,200 yds. N. 41° E. of Monkhopton Church (6330/9426).
Purple and green micaceous sandstone in cliff in southern bank of stream, 430 yds. upstream from roadbridge.
Downton Series, Red Downton Formation.

8. Besom Farm Quarry SO/68
475 yds. E. 29° S. of Besom Farm (6076/8094).
Cornstone exposed at top of old quarry, on southern side.
Ditton Series, upper group.
Pteraspis (*Cymripteraspis*) *leachi* White.
Protaspis (*Europrotaspis*) *crenulata* sp. nov.
Benneviaspis salopiensis sp. nov.
Kujdanowiaspis anglica (Traquair).
Kujdanowiaspis willsi sp. nov.
Wheathillaspis wickhamkingi gen. et sp. nov.
Ischnacanthus anglicus sp. nov.
Onchus wheathillensis sp. nov.
Onchus besomensis sp. nov.
Nodonchus bambusifer gen. et sp. nov.
Acanthodian tooth (*Plectrodus*-type).
Thelodont scales.
Acanthodian scales.
Spirorbis sp.
Pachytheca sp.

9. Bitterley Works Railway Cutting SO/57
590 yds. S. 34° E. of Bitterley Church (5740/7685).
Red sandstone in southern face of cutting, about 20 yds. from east end.
Ditton Series, lower group ; immediately overlying " *P* ". L.
Anglaspis sp.

10. Blucks House SO/68
150 yds. SW. of Blucks House (6794/8957).
Sandy cornstone exposed in stream.
Ditton Series, lower group.
Pteraspis sp.
Cephalaspis cf. *langi* Stensiö.
Cephalaspis cf. *fletti* Stensiö.
Cephalaspis cf. *agassizi* Lankester.

11. Bockleton Brook SO/58
1,030 yds. S. 13° E. of Stoke St. Milborough Church (5686/8136).
Cornstone exposed in stream, 30 yds. NE. of roadbridge.
Ditton Series, upper group ; *c.* 900 ft. above " *P* ". L.
Protaspis (*Europrotaspis*) *crenulata* sp. nov.

12. Bouldon, Clee Brook SO/58
300 yds. S. 33° E. of Bouldon Church (5484/8500).
Cornstone exposed in Clee Brook.
Downton Series, Red Downton Formation.

13. Bouldon Ford SO/58
420 yds. E. 25° S. of Bouldon Church (5496/8499).
Sandstone and cornstone exposed in stream.
Ditton Series, lower group ; *c.* 50 ft. above " *P* ". L.
Pteraspis (*Pteraspis*) *rostrata* var. *trimpleyensis* White.
Cephalaspis bouldonensis sp. nov.

14. Brockton SO/59
160 yds. N. 34° E. from crossroads at Brockton (5789/9389).
On east side of road, in bank north of gate leading into farmyard, and in farmyard.
Ludlow Bone Bed.

15. Bromdon Dingle Brook SO/58
400 yds. S. of Cleedownton (5813/8041).
Green sandy shale parting in sandstone-cornstone bluff, 30 yds. downstream from footbridge.
Ditton Series, lower group.
Pteraspis sp.
Poraspis sp.
Thelodont scales.
Acanthodian scales.
Pachytheca sp.

16. Clapgate Cottage Quarry SO/58
1,030 yds. E. 35° N. of Tugford Church (5650/8756).
Cornstone in old quarry, 40 yds. from road.
Ditton Series, lower group ; *c.* 110 ft. above " *P* ". L.
Pteraspis cf. (*Simopteraspis*) *leathensis* White.
Traquairaspis symondsi (Lankester).
Anglaspis sp.
Tesseraspis sp.
? Cephalaspid.
Acanthodian scales, spines and jaws.
Thelodont scales.

17. Clee St. Margaret SO/58
630 yds. N. 38° W. of Clee St. Margaret Church (5609/8480).
Green sandstone and cornstone in eastern bank of stream section.
Ditton Series, lower group ; *c.* 675 ft. above " *P* ". L.
Pteraspis (*Belgicaspis*) *crouchi* var. *heightingtonensis* White.
Anglaspis sp.
Cephalaspid.
Arctolepid.

18. Cold Weston Quarry SO/58
490 yds. W. 8° N. of Cold Weston Church (5474/8309).
Old quarry.
Ditton Series, lower group ; *c.* 850 ft. above " *P* ". L.
? Arctolepid.

19. Criddon Bridge SO/69
1,620 yds. E. 36° S. of Upton Cresset Church (6681/9159).
Red silty sandstone outcropping in stream.
Ditton Series, lower group ; 5 ft. above " *P* ". L.
cf. *Kujdanowiaspis* sp.
Modiolopsis sp.

20. Dairy Dingle SO/68
1,425 yds. E. 3° S. of Neenton Church (6503/8767).
Cornstone exposed in stream.
Ditton Series, lower group ; *c.* 800 ft. above " *P* ". L.
Pteraspis (*Pteraspis*) *dairydinglensis* sp. nov.
Acanthodian scales.
Thelodont scales.
Cephalaspid.
Indet. spine.
Pachytheca sp.

21. Derrington Rea Bridge SO/69
500 yds. SE. of Derrington (6099/9052).
Cornstone exposed in stream section, 20 yds. downstream from bridge.
Ditton Series, lower group ; *c.* 500 ft. above " *P* ". L.
Pteraspis (*Pteraspis*) *dairydinglensis* sp. nov.
Thelodont scales.
Acanthodian scales.
Cephalaspid.

22. Devil's Mouthpiece Quarry SO/58
1,850 yds. E. 43° N. of Upper Hayton Church (5303/8210).
Sandstone and cornstone in old quarry.
Ditton Series, lower group ; *c.* 400 ft. above " *P* ". L.

23. Dodshill Bank SO/58
630 yds. S. 23° W. of the Three Horseshoes Inn (5978/8138).
Grey and buff silty sandstone in small quarry.
Ditton Series, ? upper group.
Prototaxites sp.
Pachytheca sp.
Nematothallus sp.
cf. *Cooksonia* sp.

24. Down Quarry, The SO/68
350 yds. S. 10° E. of The Down (6374/8157).
Cornstone exposed in old quarry, largely overgrown.
Ditton Series, upper group.
Pteraspis ? (*Cymripteraspis*) sp.
Protaspis (*Europrotaspis*) *crenulata* sp. nov.

25. Earnstrey Brook (Leath 3) SO/58
570 yds. N. 11° E. of Earnstrey Hall (5752/8889).
Massive cornstone forming waterfall, and grey marl immediately underlying it (see also Wills, 1935 : 427 ; White, 1946 : 210).
Downton Series, Red Downton Formation ; *c.* 70 ft. below " *P* ". L.
Traquairaspis symondsi (Lankester).
Anglaspis macculloughi A. S. Woodward.
Corvaspis kingi A. S. Woodward.
Tesseraspis tessellata Wills.
Cephalaspis sp.
Onchus sp.
Pachytheca sp.

26. Earnstrey Hall 1 SO/58
510 yds, E. 7° N. of Earnstrey Hall (5787/8825).
Red sandstone exposed in stream, 70 yds. downstream from road.
Ditton Series, lower group ; *c.* 400 ft. above " *P* ". L.
Pteraspis (*Belgicaspis*) *crouchi* Lankester.

27. Earnstrey Hall 2 SO/58
600 yds. E. 6° S. of Earnstrey Hall (5794/8826).
Sandstone exposed immediately below bridge.
Ditton Series, lower group ; *c.* 420 ft. above " *P* ". L.
Pteraspis cf. (*Belgicaspis*) *crouchi* Lankester.

28. Farlow Brook Bridge SO/68
325 yds. N. 32° W. of Farlow Church (6380/8088).
Cornstone exposed in bank on south side of lane.
Ditton Series, upper group.
Pteraspis ? (*Cymripteraspis*) *leachi* White.
Protaspis (*Europrotaspis*) *crenulata* sp. nov.
Arctolepid.
" Ichthyodorulite."

29. Farlow, Old Lane SO/68
160 yds. E. 35° N. of Farlow Church (6408/8071).
Sandstones exposed on south side of cutting, about half-way down old lane.
Yellow Farlow Sandstone Series.
Crossopterygian indet.

30. Fox Covert SO/68
720 yds. E. 20° N. of Wheathill Church (6283/8237).
Cornstone poorly exposed in stream.
Ditton Series, upper group.

31. Foxhole Coppice, Monkhopton SO/69
910 yds. E. 25° S. of Monkhopton Church (6180/9308).
Cornstone forming waterfall.
Downton Series, Red Downton Formation ; 25 ft. below " *P* ". L.
Kallostrakon sp.
Acanthodian scales, jaws and spines.

32. Foxhole Coppice, Newton Dingle SO/58
1,650 yds. W. 9° S. of the Three Horseshoes Inn (5849/8168).
Red and green cornstone and sandstone exposed in cliff above east bank of stream.
Ditton Series, lower group ; *c.* 750 ft. above " *P* ". L.

33. Great Northwood SO/68
60 yds. ESE. of Great Northwood (6798/8410).
Old quarry.
Ditton Series, upper part of lower group.
Pteraspis cf. (*Belgicaspis*) *crouchi* Lankester.

34. Heath Quarry SO/58
230 yds. W. 15° N. of Heath Church (5551/8570).
Cornstone exposed at western end of old water-filled quarry.
Ditton Series, lower group ; *c.* 300 ft. above " *P* ". L.
Pteraspis (*Belgicaspis*) *crouchi* Lankester.
? *Weigeltaspis* or *Tesseraspis* sp.

35. Hills, The SO/57
? 1,230 yds. E. 20° S. of Downton Hall (5386/7895) ; a classic locality, the exact position of which is uncertain.
Old quarry.
Ditton Series, lower group.
Pteraspis (*Belgicaspis*) *crouchi* Lankester.
Cephalaspis sp.
Acanthodian.

36. Hoptongate SO/58
2,040 yds. W. 2° N. of Hopton Cangeford Church (5299/8047).
Old quarry.
Ditton Series, lower group ; *c.* ? 700 ft. above " *P* ". L.
Pteraspis sp.
Kujdanowiaspis anglica (Traquair).

37. Hudwick Dingle 1 SO/69
980 yds. S. 39° E. of Monkhopton Church (6314/9274).
Thick cornstone immediately overlying the " *P* ". L. at the confluence of Hudwick and Stapeley Dingles.
Ditton Series, lower group ; immediately overlying " *P* ". L.
Pteraspis ? (*Simopteraspis*) *leathensis* White.
Traquairaspis symondsi (Lankester).
Anglaspis sp.
Tesseraspis sp.
Corvaspis kingi A. S. Woodward.
Ischnacanthus wickhami sp. nov.
Acanthodian scales (cf. *Gomphodus* sp. and *Nostolepis* sp.) and spine.
Thelodont scales.
Cephalaspid.
Pachytheca sp.

38. Hudwick Dingle 2 SO/69
1,700 yds. S. 28° E. of Monkhopton Church (6330/9206).
Pavement of cornstone exposed a few yards below confluence of streams.
Ditton Series, lower group ; *c.* 250 ft. above " *P* ". L.
Pteraspis sp.

39. HUDWICK DINGLE 3 SO/69
1,310 yds. S. 34° E. of Monkhopton Church (6323/9243).
Purple and green cornstone and sandstone in west bank of stream.
Ditton Series, lower group ; *c.* 80 ft. above " *P* ". L.
Pteraspis (*Simopteraspis*) *leathensis* White.

40. HUDWICK DINGLE 4 SO/69
1,510 yds. S. 32° E. of Monkhopton Church (6329/9224).
Grey-green cornstone outcropping 10 ft. above base of thick cornstone-sandstone series, forming rapids and waterfall.
Ditton Series, lower group ; *c.* 175 ft. above " *P* ". L.
Pteraspis (*Pteraspis*) *rostrata* (Agassiz) var. indet.
Cephalaspid.
Thelodont scales.
Acanthodian.
Pachytheca sp.

41. HUDWICK DINGLE 5 SO/69
2,190 yds. S. 29° E. of Monkhopton Church (6353/9168).
Red and green cornstone exposed in stream, 175 yds. upstream from footbridge.
Ditton Series, lower group ; *c.* 400 ft. above " *P* ". L.
Pteraspis sp.
Acanthodian scales.
Pachytheca sp.

42. JUBILEE BROOK 1 SO/57
500 yds. W. 35° N. of Upper Ledwyche (5503/7948).
Green sandstone exposed in stream.
Ditton Series, lower group ; *c.* 250 ft. above " *P* ". L.
Pteraspis (*Pteraspis*) *rostrata* var. *waynensis* White.
Poraspis sp.
? *Corvaspis* sp.
Acanthodian spine.

43. JUBILEE BROOK 2 SO/57
460 yds. W. 22° N. of Upper Ledwyche (5501/7938).
Stream section.
Ditton Series, lower group.

44. KIDNALL GUTTER 1 SO/58
870 yds. S. 15° W. of Tugford Church (5551/8628).
Red cornstone exposed in stream.
Ditton Series, lower group ; 15 ft. above " *P* ". L.
Pteraspis (*Pteraspis*) *rostrata* (Agassiz) var. indet.
Cephalaspid.
Thelodont scales.
Acanthodian scales.

45. Kidnall Gutter 1a
875 yds. S. 13° W. of Tugford Church (5554/8627).
Cornstone exposed in stream.
Ditton Series, lower group ; *c.* 30 ft. above " *P* ". L.
Pteraspis (*Simopteraspis*) *leathensis* White.
? *Traquairaspis* sp.
Acanthodian spines.

46. Kidnall Gutter 2 SO/58
880 yds. S. 12° W. of Tugford Church (5556/8626).
Cornstone exposed in stream.
Ditton Series, lower group ; *c.* 75 ft. above " *P* ". L.
Pteraspis (*Pteraspis*) *rostrata* cf. var. *trimpleyensis* White.

47. Kidnall Gutter 3 SO/58
890 yds. S. 4° W. of Tugford Church (5567/8625).
Cornstone exposed in stream.
Ditton Series, lower group ; *c.* 180 ft. above " *P* ". L.
Pteraspis (*Belgicaspis*) *crouchi* Lankester.
Pteraspis ? sp. nov.
Cephalaspid.
Thelodont scales.
Acanthodian scales and spines.

48. Kidnall Gutter 4 SO/58
900 yds. S. 2° W. of Tugford Church (5570/8625).
Grey, brown and red mottled sandstone with cornstone lenses, exposed in stream section.
Ditton Series, lower group ; *c.* 200 ft. above " *P* ". L.
Pteraspis sp.
? *Tesseraspis* sp.
Thelodont scales.
Acanthodian scales.
Pachytheca sp.

49. Leath 1 SO/58
30 yds. E. of Leath Cottage (5846/8989).
Deep gulley running parallel with road, on north side of Leath Bank (see also White 1950*a* : 70, 71).
? Ditton Series, lower group.
Pteraspis (*Simopteraspis*) *leathensis* White.
Cephalaspid.
Pachytheca sp.

50. Ledwyche Brook SO/58
1,480 yds. E. 9° S. of Hopton Cangeford Church (5620/8018).
Cornstone exposed in west bank of stream, 180 yds. downstream from ford.
Ditton Series, lower group ; *c.* 60 ft. above " *P* ". L.
Pteraspis (*Pteraspis*) *rostrata* var. *trimpleyensis* White.
Cephalaspid.
Acanthodian scales and spine.
Thelodont scales.

51. Little Oxenbold SO/59
540 yds. SE. of Little Oxenbold (5906/9117).
Purple and green cornstone and marls exposed in stream section.
Downton Series, Red Downton Formation ; 50 ft. below " *P* ". L.
Traquairaspis symondsi (Lankester).
Anglaspis sp.
Corvaspis sp.
Tesseraspis sp.
Acanthodian.

52. Lowe Farm Quarry SO/68
150 yds. S. 19° W. of Lowe Farm (6310/8034).
Cornstone exposed in small overgrown quarry.
Ditton Series, ? upper group.
Pteraspis sp.
? Arctolepid.

53. Lower Ingardine Ford SO/68
780 yds. S. 35° E. of Wheathill Church (6250/8150).
Very coarse cornstone exposed in stream.
Ditton Series, upper group.
Pteraspis (*Cymripteraspis*) *leachi* White.
Protaspis (*Europrotaspis*) *crenulata* sp. nov.
cf. *Kujdanowiaspis anglica* (Traquair).
Arctolepid.
Cephalaspid.
Thelodont scales.

54. Lydehole SO/58
1,150 yds. N. 38° E. of Upper Hayton Church (5244/8179).
Grey-buff cornstone exposed in stream section.
Ditton Series, lower group ; *c.* 130 ft. above " *P* ". L.
Pteraspis sp.

55. Lye Brook 1 SO/69
1,050 yds. S. 19° E. of Morville Church (6728/9298).
Cornstone exposed in stream, forming waterfall.
Downton Series, Red Downton Formation ; 125 ft. below " *P* ". L.
Traquairaspis symondsi (Lankester).
Cephalaspid.
Acanthodian spines.

56. Lye Brook 2 SO/69
1,140 yds. S. 11° E. of Morville Church (6717/9287).
Block of green cornstone in stream, uncertain whether *in situ*.
Stratigraphical position uncertain, but the locality is below " *P* ". L.
Pteraspis (*Simopteraspis*) *leathensis* White.
Acanthodian spine.

57. Lye Brook 3 SO/69
1,100 yds. S. 15° E. of Morville Church (6723/9290).
Cornstone outcropping about 1½ ft. above waterfall formed by mudstone and fine calcareous sandstones.
Downton Series, Red Downton Formation ; *c.* 90 ft. below " *P* ". L.
Traquairaspis symondsi (Lankester).
Thelodont scales.
Acanthodian scales.
Cephalaspid scales.

58. Lye Brook 4 SO/69
1,180 yds. S. 4° E. of Morville Church (6703/9281).
Cornstone outcropping in stream, forming waterfall.
Ditton Series, lower group ; 75 ft. above " *P* ". L.
Pteraspis (*Simopteraspis*) *leathensis* White.
Poraspis sp.

59. Middleton Priors SO/69
210 yds. N. 9° W. of Middleton Priors School (6235/9049).
Cornstone exposed in stream section, 20 yds. above bridge.
Ditton Series, lower group ; *c.* 500 ft. above " *P* ". L.
Pteraspis (*Belgicaspis*) *crouchi* Lankester.
Acanthodian scales.
Thelodont scales.

60. Mill Farm Bridge SO/68
210 yds. E. 30° S. of Mill Farm (6408/8127).
Cornstone exposed in cutting on east side of road.
Ditton Series, upper group.
Pteraspis ? (*Cymripteraspis*) *leachi* White.
Thelodont scales.

61. Munslow SO/58
820 yds. E. 12° N. of Munslow Church (5286/8787).
Ludlow Bone Bed.

62. Netchwood Common SO/69
2,260 yds. S. 13° W. of Monkhopton Church (6202/9110).
Cornstone exposed in stream section.
Ditton Series, lower group ; *c.* 400 ft. above " *P* ". L.
Pteraspis (*Belgicaspis*) *crouchi* Lankester.

63. New Buildings A SO/58
510 yds. S. 38° E. of New Buildings (5796/9898).
Grey-green cornstone exposed at top of gully.
Ditton Series, lower group.

64. New Buildings B SO/58
500 yds. E. 22° S. of New Buildings (5808/8918).
Large blocks of grey-green cornstone in field.
Ditton Series, lower group ; blocks not *in situ.*
Pteraspis cf. (*Belgicaspis*) *crouchi* Lankester.

65. New Buildings C SO/58
475 yds. E. of New Buildings (5810/8934).
Grey cornstone outcropping half-way up escarpment.
Ditton Series, lower group.

66. New Buildings D SO/58
290 yds. S. 37° E. of New Buildings (5781/8914).
Red sandstone exposed in stream near foot of escarpment.
Downton Series, Red Downton Formation ; 110 ft. below " *P* ". L.
Indet. spine.

67. New Buildings E/2 SO/58
590 yds. S. 17° E. of New Buildings (5782/8882).
Red and green sandstone and cornstone exposed at top of stream section.
Ditton Series, lower group ; *c.* 110 ft. above " *P* ". L.
Pteraspis (*Pteraspis*) *rostrata* (Agassiz).

68. New Buildings E/3 SO/58
320 yds. S. 34° E. of New Buildings (5784/8912).
Cornstone exposed in stream section.
Downton Series, Red Downton Formation ; *c.* 75 ft. below " *P* ". L.
Traquairaspis symondsi (Lankester).
Anglaspis sp.
Acanthodian spines.

69. New Buildings E/3A SO/58
430 yds. S. 35° E. of New Buildings (5789/8904).
Cornstone exposed in stream section.
Ditton Series, lower group ; 2 ft. above " *P* ". L.
Pteraspis sp.

70. New Buildings F SO/58
570 yds. E. 27° S. of New Buildings (5817/8910).
Green sandy cornstone exposed in stream section.
Ditton Series, lower group ; *c.* 175 ft. above " *P* ". L.

71. New Inn 1 SO/58
1,440 yds. W. 43° S. of Upper Hayton Church (5092/8012).
Cornstone forming waterfall in stream, 640 yds. above road.
Downton Series, Red Downton Formation ; 16 ft. below " *P* ". L.
Pteraspis (*Simopteraspis*) *leathensis* White.
Traquairaspis symondsi (Lankester).
Poraspis sp.
Tesseraspis sp.
Cephalaspid.
Acanthodian spines and teeth.
Thelodont scales.
Pachytheca sp.

72. New Inn 2 SO/58
1,260 yds. S. 44° W. of Upper Hayton Church (5099/8012).
Cornstone forming waterfall in stream, 700 yds. above road.
Ditton Series, lower group ; *c.* 75 ft. above " *P* ". L.
Pteraspis (*Simopteraspis*) *leathensis* White.
Poraspis sp.
Anglaspis sp.
Acanthodian scales, spines and teeth.
Thelodont scales.
Pachytheca sp.

73. Newton Dingle 1 SO/58
520 yds. W. 40° N. of the Three Horseshoes Inn (5963/8221).
Cornstone exposed in eastern bank of stream.
Ditton Series, upper group ; *c.* 900 ft. above " *P* ". L.
Pteraspis (*Cymripteraspis*) sp.
Kujdanowiaspis anglica (Traquair).

74. Newton Dingle 2 SO/58
700 yds. N. 9° W. of the Three Horseshoes Inn (5990/8254).
Cornstone exposed in stream section immediately below lane.
Ditton Series, upper group ; *c.* 950 ft. above " *P* ". L.
Pteraspis ? (*Cymripteraspis*) *leachi* White.
Protaspis (*Europrotaspis*) *crenulata* sp. nov.
Arctolepid.
Acanthodian scales and spine.
Thelodont scales.

75. Oak Dingle SO/58
920 yds. E. 4° N. of Tugford Church (5656/8712).
Red sandstone exposed in stream, 100 yds. upstream from road.
Ditton Series, lower group ; *c.* 125 ft. above " *P* ". L.
Pteraspis (*Pteraspis*) *rostrata* var. *trimpleyensis* White.
Traquairaspis symondsi (Lankester.)
Tesseraspis sp.
Cephalaspis sp.
Acanthodian spine.
Thelodont scale.

76. Oldfield, The Lobby SO/68
140 yds. S. of The Lobby (6710/8850).
Green sandy cornstone exposed in stream.
Ditton Series, lower group.
Pteraspis (*Belgicaspis*) *crouchi* Lankester.

77. Old Forge Quarry SO/58
330 yds. S. 35° E. of Bouldon Church (5488/8489).
Sandstones and cornstones in old quarry.
Ditton Series, lower group.

78. Park Barn Quarry SO/58
850 yds. E. 29° N. of Tugford Church (5639/8744).
Red cornstone exposed in old quarry, 70 yds. from road.
Ditton Series, lower group ; *c.* 80 ft. above " *P* ". L.
Pteraspis sp.
Tesseraspis sp.
Cephalaspid scales.
Thelodont scales.
Acanthodian scales and spines.

79. Park Dingle SO/69
2,460 yds. S. 35° E. of Monkhopton Church (6386/9158).
Green sandstone and shales with pellet bands, exposed in stream section and forming waterfall.
Ditton Series, lower group.

80. PARLOUR COPPICE SO/69
660 yds. W. 7° N. of Upton Cresset Church (6500/9253).
Cornstone exposed in stream section.
Ditton Series, lower group ; *c.* 400 ft. above " *P* ". L.
Tesseraspis sp.

81. POSTON OLD QUARRY SO/58
1,300 yds. N. 17° W. of Hopton Cangeford Church (5452/8154).
Cornstone and sandstone in old quarry.
Ditton Series, lower group ; *c.* 800 ft. above " *P* ". L.
Pteraspis sp.
Arctolepids.

82. PRESCOTT CORNER SO/68
110 yds. N. of Prescott Farm (6636/8118).
Sandstones exposed in south side of bank at sharp bend in road, 5 ft. above road surface.
Yellow Farlow Sandstone Series.
Bothriolepis sp.
Holoptychius sp.
Pseudosauripterus anglicus (A. S. Woodward).
? *Eusthenopteron farloviensis* sp. nov.
Indet. Crossopterygii.

83. PRESCOTT, OLD LANE SO/68
175 yds. S. 15° W. of Prescott Farm (6632/8092).
Pellety sandstones exposed below hedge on east side of lane.
Grey Farlow Sandstone Series.

84. PRESCOTT, REASIDE SO/68
300 yds. N. 35° W. of Prescott Farm (6622/8129).
Cornstone exposed in east bank of river.
Ditton Series, upper group ; ? *c.* 1,100 ft. above " *P* ". L.
Pteraspis (*Cymripteraspis*) *leachi* White.
Protaspis (*Europrotaspis*) *crenulata* sp. nov.
Kujdanowiaspis cf. *anglica* (Traquair).
Prescottaspis dineleyi gen. et sp. nov.
Thelodont scales.
Pachytheca sp.

85. REA BRIDGE, DITTON PRIORS SO/68
1,650 yds. E. 28° N. of Ditton Priors Church (6216/8985).
Loose blocks of cornstone in field.
Ditton Series, lower group ; not *in situ*.
Pteraspis (*Pteraspis*) *rostrata* (Agassiz) var. indet.

86. Rea Brook, New House Farm SO/68
160 yds. W. of New House Farm (6375/8810).
Cornstone exposed in banks of stream.
Ditton Series, lower group ; ? *c.* 650 ft. above " *P* ". L.
Kujdanowiaspis anglica (Traquair).

87. Shipton SO/59
160 yds. E. 42° S. of Shipton Church (5630/9176).
Exposure in sides of lane.
Ludlow Bone Bed.

88. Shortwood SO/57
1,300 yds. W. 30° S. of Downton Hall (5179/7870).
Old quarry.
Ditton Series, lower group.

89. Silvington Church SO/67
Cornstone exposed on west side of road near to churchyard gate (6215/7984).
Ditton Series.

90. Silvington, Drainage Gully SO/68
550 yds. N. 30° W. of Cleeton Court (6094/8002).
Cornstone exposed in drainage gully.
Ditton Series, lower group ; ? *c.* 575 ft. above " *P* ". L.
Pteraspis cf. (*Belgicaspis*) *crouchi* Lankester.

91. Silvington, Old Quarry 1 SO/68
175 yds. N. 6° E. of Silvington Church (6216/8002).
Cornstone exposed in old quarry.
Ditton Series.
Pteraspis sp.

92. Silvington, Old Quarry 2 SO/68
270 yds. NE. of Silvington Church (6231/8003).
Cornstone exposed in old quarry.
Ditton Series.
cf. *Climatius* sp.

93. Silvington, Upper Quarry SO/68
1,630 yds. S. 20° E. of Wheathill Church (6272/8076).
Massive cornstone, 14 ft.+ thick, exposed in old quarry.
Ditton Series, upper group.
Pteraspis ? (*Cymripteraspis*) *leachi* White.

94. SILVINGTON, WATERFALL SO/67
1,250 yds. W. 5° N. of Silvington Church (6096/7994).
Cornstone exposed in north bank of stream, 5 yds. upstream from waterfall.
Ditton Series, lower group ; ? *c.* 600 ft. above " *P* ". L.
Pteraspis (*Belgicaspis*) *crouchi* var. *heightingtonensis* White.
? *Tesseraspis* sp.
Kujdanowiaspis anglica (Traquair).
Arctolepid.
Cephalaspid.
Acanthodian.

95. STAPELEY DINGLE SO/69
990 yds. SE. of Monkhopton Church (6320/9279).
Red and green cornstone immediately overlying " *P* ". L. and forming first waterfall above the confluence with Hudwick Dingle.
Ditton Series, lower group ; immediately overlying " *P* ". L.

96. STOTTESDON BROOK SO/68
1,150 yds. S. of Stottesdon Church (6724/8184).
Cornstone exposed in stream.
Ditton Series, upper group ; ? *c.* 1,100 ft. above " *P* ". L.
Pteraspis ? (*Cymripteraspis*) *leachi* White.
Protaspis ? (*Europrotaspis*) *crenulata* sp. nov.
? *Kujdanowiaspis* sp.
Thelodont scale.

97. SUDFORD DINGLE 1 SO/69
780 yds. S. 9° E. of Monkhopton Church (6268/9273).
Grey-green sandy cornstone exposed in stream.
Ditton Series, lower group ; 3–4 ft. above " *P* ". L.
Traquairaspis symondsi (Lankester).

98. SUDFORD DINGLE 2 SO/69
1,250 yds. S. 11° W. of Monkhopton Church (6235/9230).
Pavement of cornstone at confluence of streams.
Ditton Series, lower group ; *c.* 170 ft. above " *P* ". L.
Pteraspis (*Belgicaspis*) *crouchi* Lankester.

99. TARGROVE DINGLE 1 SO/57
910 yds. E. 25° N. of Whitbatch (5251/7789).
Red cornstone exposed in stream section, 140 yds. below drive to Downton Hall.
Ditton Series, lower group ; 18 ft. above " *P* ". L.
Anglaspis sp.

100. TARGROVE DINGLE 2 SO/57
930 yds. E. 30° N. of Whitbatch (5249/7795).
Red and green cornstone and sandstone exposed in stream, 40 yds. below drive to Downton Hall.
Ditton Series, lower group.
Pteraspis sp.

101. TARGROVE DINGLE 3 SO/57
900 yds. E. 36° N. of Whitbach (5243/7803).
Red and green cornstone forming waterfall near top of western tributary, 60 yds. above drive to Downton Hall.
Ditton Series, lower group ; *c.* 250 ft. above " *P* ". L.
Pteraspis (*Belgicaspis*) *crouchi* Lankester.

102. TARGROVE DINGLE 4 SO/57
920 yds. E. 23° N. of Whitbatch (5253/7787).
Cornstone forming waterfall, 160 yds. below drive to Downton Hall.
Downton Series, Red Downton Formation ; 6 ft. below " *P* ". L.

103. TARGROVE DINGLE 5 SO/57
920 yds. E. 28° N. of Whitbatch (5250/7793).
Cornstone forming waterfall, 78 yds. below drive to Downton Hall.
Ditton Series, lower group.

104. TARGROVE DINGLE 6 SO/57
1,030 yds. E. 13° N. of Whitbatch (5266/7775).
Red calcareous mudstone outcropping in stream section 330 yds. below drive.
Downton Series, Red Downton Formation ; *c.* 100 ft. below " *P* ". L.
Kallostrakon sp.
" *Onychodus*."
Acanthodian.
Anaspid.

105. TARGROVE QUARRY SO/57
1,000 yds. E. 31° N. of Whitbatch (5254/7799).
Old quarry on north side of drive to Downton Hall.
Ditton Series, lower group ; *c.* 175 ft. above " *P* ". L.
Pteraspis (*Pteraspis*) *rostrata* var. *trimpleyensis* White.
Traquairaspis symondsi (Lankester).
Acanthodian scales.
Thelodont scales.

106. THRIFT, THE	SO/58

900 yds. S.27° E. of Clee St. Margaret Church (5682/8363).
Cornstone exposed in west bank of road, 200 yds. south of Burnt House.
Ditton Series, upper group ; *c.* 1,300 ft. above " *P* ". L.
Pteraspis ? (*Cymripteraspis*) *leachi* White.

107. UPPER LEDWYCHE, OLD QUARRY	SO/57

600 yds. W. 11° N. of Upper Ledwyche (5488/7933).
Cornstone outcropping in old quarry.
Ditton Series, lower group ; ? *c*, 200 ft. above " *P* ". L.
Pteraspis sp.

108. UPPER OVERTON QUARRY	SO/68

100 yds. N. 30° W. of Upper Overton (6647/8688).
Cornstones in quarry, now overgrown and in cutting on south side of quarry.
Ditton Series, upper group ; ? *c.* 900 ft. above " *P* ". L.
Pteraspis ? (*Cymripteraspis*) *leachi* White.
Protaspis (*Europrotaspis*) *crenulata* sp. nov.
Overtonaspis billballi gen. et sp. nov.
? *Kujdanowiaspis* sp.
? *Wheathillaspis* sp.
Cephalaspid.
Thelodont scales.
Acanthodian scales.

109. UPTON CRESSET QUARRY	SO/69

150 yds. N. of Upton Cresset Church (6560/9259).
Purple cornstone exposed in old quarry.
Ditton Series, lower group ; *c.* 400 ft. above " *P* ". L.
Pteraspis cf. (*Pteraspis*) *dairydinglensis* sp. nov.
Cephalaspid scales and fragments.
Acanthodian scales and spine.
Thelodont scales.

110. UPTON LODGE QUARRY	SO/69

1,360 yds. S. 12° E. of Upton Cresset Church (6586/9124).
Cornstone exposed in old quarry.
Ditton Series, lower group.
Indet. spine.

111. WALLSBATCH QUARRY	SO/68

1,300 yds. E. 35° N. of Faintree Hall (6720/8965).
Cornstone exposed in old quarry.
Ditton Series, lower group.

112. WALTON BROOK 1 SO/68
710 yds. S. 31° E. of Prescott Farm (6670/8051).
Sandy cornstone exposed in stream.
Grey Farlow Sandstone Series.
Holoptychius sp.

113. WALTON BROOK 2 SO/68
800 yds. S. 37° E. of Prescott Farm (6680/8048).
Grey calcareous sandy pebbly cornstone exposed in stream.
Grey Farlow Sandstone Series.

114. WALTON QUARRY SO/68
175 yds. N. 15° W. of Walton (6757/8138).
Pellety sandstone at foot of quarry face.
Ditton Series, upper group ; immediately beneath lower Abdon Limestone ; *c.* 1,450 ft. above " *P* ". L.
Arctolepid.
Acanthodian scale.

115. WHITBATCH LANE SO/57
200 yds. E. 12° N. of Whitbatch (5193/7759).
Exposure in roadside at sharp angle in lane.
Downton Series, Red Downton Formation.
Cephalaspis sp.

116. WHITBATCH QUARRY SO/57
300 yds. NE. of Whitbatch (5195/7776).
The fauna listed probably comes from more than one locality, but mainly from old quarry.
Ditton Series, lower group ; *c.* 200 ft. above " *P* ". L.
Pteraspis (*Pteraspis*) *rostrata* (Agassiz).
Cephalaspis fletti Stensiö.
Cephalaspis whitbatchensis Stensiö.
Cephalaspis whitei Stensiö.
Cephalaspis lankesteri Stensiö.
Cephalaspis acutirostris Stensiö.
Cephalaspis ? sp. nov.

117. WILDERNESS SO/58
500 yds. E. 35° S. of Ashfield (5911/8917).
Cornstone exposed in stream, 40 yds. south of roadbridge.
Ditton Series, lower group ; *c.* 500 ft. above " *P* ". L.

118. WINTERBURN BRIDGE SO/68
950 yds. NW. of Upper Overton (6592/8740).
Cornstone exposed below bridge.
Ditton Series, ? top of lower group.
Pteraspis sp.
Cephalaspid.
Acanthodian scales.
Thelodont scales.

119. WITCHCOT-POSTON DINGLES SO/58
1,120 yds. N. 39° W. of Hopton Cangeford Church (5421/8124).
Sandstone and cornstone exposed in scar on east bank, near confluence of Witchcot and Poston Dingles.
Ditton Series, lower group ; *c.* 800 ft. above " *P* ". L.
Pteraspis sp.

120. WOODHOUSE QUARRY SO/57
? 1,400 yds. W. 16° N. of Downton Hall (5157/7967).
Cornstones exposed in old quarry.
Ditton Series, lower group.

121. YEWTREE DINGLE SO/69
1,200 yds. W. 22° S. of Morville Church (6596/9348).
Green calcareous sandstone and cornstone, exposed amongst roots of tree at head of dingle.
Ditton Series, lower group ; *c.* 50 ft. above " *P* ". L.
Pteraspis (*Simopteraspis*) *leathensis* White.

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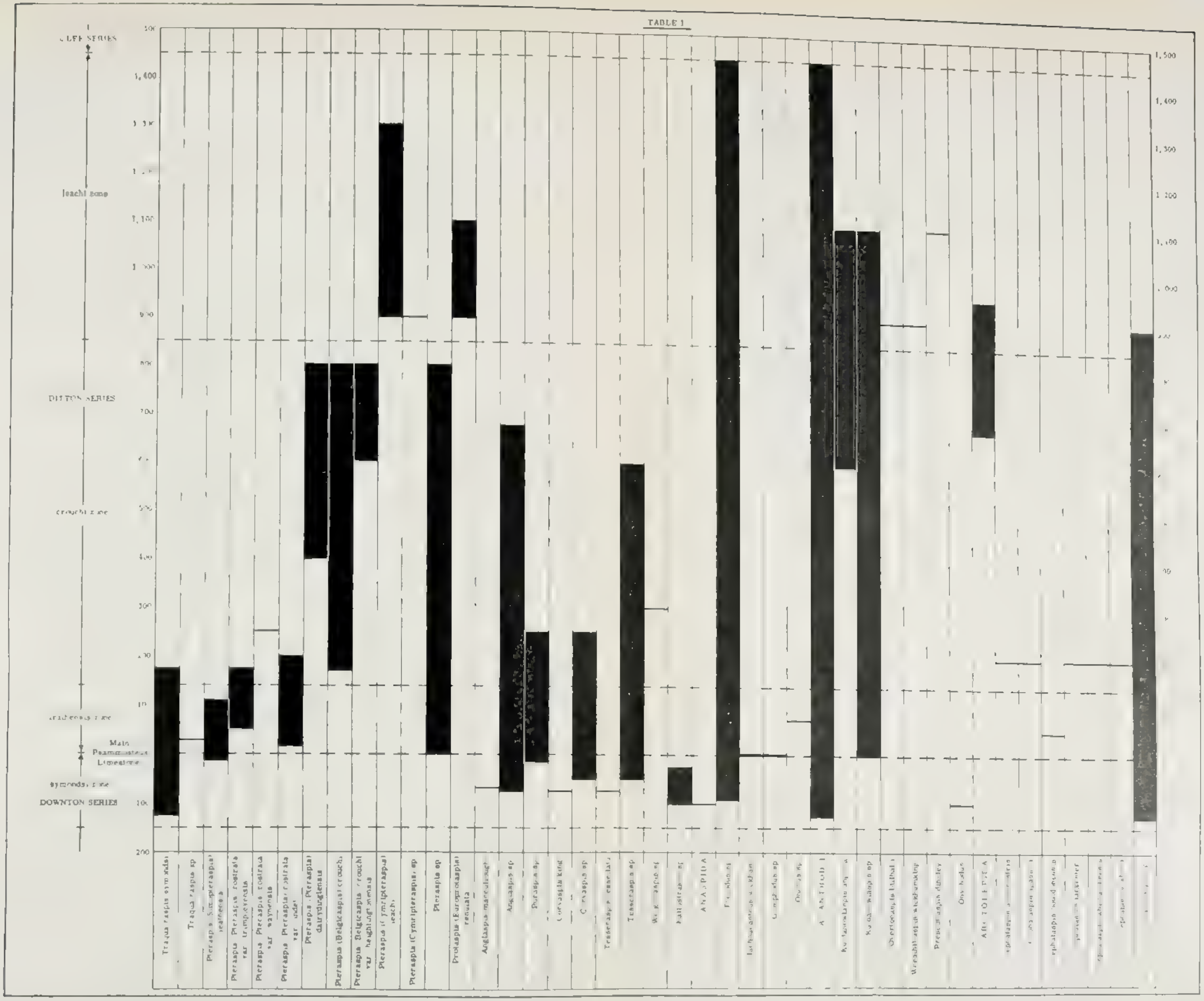
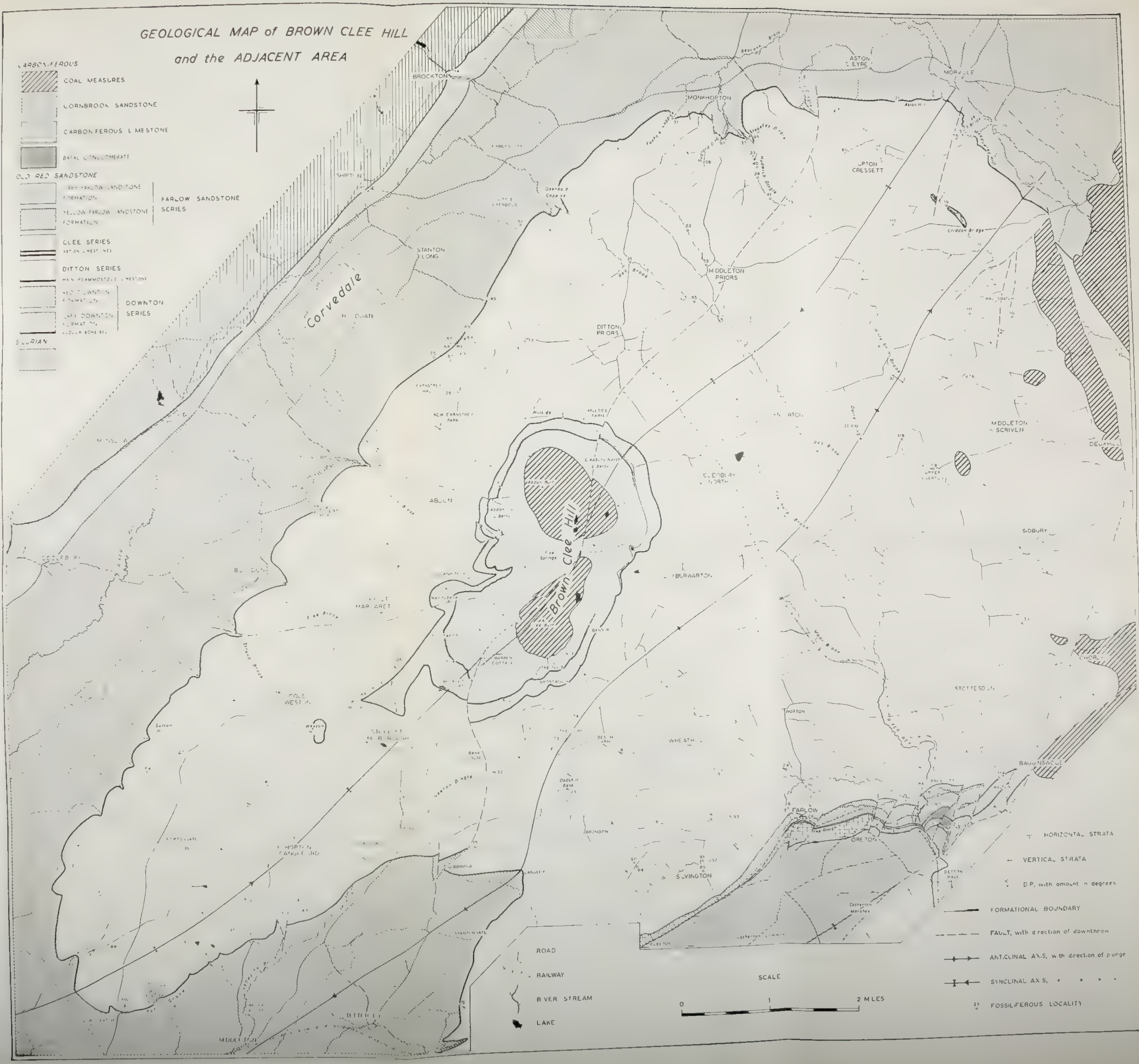


TABLE 1 Range chart of uppermost Downtonian and Dittonian vertebrate faunas in the area of Brown Clee Hill. The ranges given in the Table are compiled only from localities whose position relative to the main "*Psammosteus*" Limestone can be calculated. Thus they do not represent the absolute ranges of the forms listed.


GEOLOGICAL MAP of BROWN CLEE HILL
and the ADJACENT AREA
CARBONIFEROUS
COAL MEASURES
CORNBROOK SANDSTONE
CARBONIFEROUS LIMESTONE
BASAL CONGLOMERATE
OLD RED SANDSTONE
GREY FARLOW SANDSTONE FORMATION
YELLOW FARLOW SANDSTONE FORMATION
FARLOW SANDSTONE SERIES
CLEE SERIES
ABDON LIMESTONES
DITTON SERIES
MAIN PSAMMOSTEUS LIMESTONE
RED DOWNTON FORMATION
GREY DOWNTON FORMATION
LUDLOW BONE BED
DOWNTON SERIES
SILURIAN
HORIZONTAL STRATA
VERTICAL STRATA
DIP, with amount in degrees
FORMATIONAL BOUNDARY
FAULT, with direction of downthrow
ANTICLINAL AXIS, with direction of plunge
SYNCLINAL AXIS, " " " "
FOSSILIFEROUS LOCALITY
ROAD
RAILWAY
RIVER STREAM
LAKE
SCALE
0
1
2 MILES
BROCKTON
MONKHOPTON
ASTON EYRE
MORVILLE
SHIPTON
UPTON CRESSETT
STANTON LONG
Corvedale
MIDDLETON PRIORS
DITTON PRIORS
Brown Clee Hill
ABDON
CLEOBURY NORTH
BURWARTON
MIDDLETON SCRIVEN
SIDBURY
STOTTESDON
WHEATHILL
FARLOW
ORETON
SILVINGTON
BAGGINSWOOD
COLD WESTON
HOPTON CANGEFORD
BITTERLEY
MIDDLETON
Criddon Bridge
Aston Hill
Cutherton Marshes

PART II. PALAEONTOLOGY

By ERROL IVOR WHITE

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I. FAUNA OF THE UPPER PART OF THE RED DOWNTON FORMATION AND THE LOWER GROUP OF THE DITTON SERIES

UNDER this heading are grouped all the elements found in the zones of *Traquairaspis symondsi*, *Pteraspis leathensis* and *P. crouchi*, since, as Drs. Ball and Dineley have explained in Part I of the paper (pp: 201–202) most elements of the *T. symondsi* Zone pass, although in greatly reduced numbers, into the succeeding zone and, from the systematic viewpoint, may therefore be conveniently dealt with together.

Throughout the text, the heights given are relative to the main "*Psammosteus*" Limestone. The numbers in parentheses refer to registered speciemens in the British Museum (Natural History) collections.

Class AGNATHA

Order HETEROSTRACI

Genus ***KALLOSTRAKON*** Lankester, 1870

Kallostrakon sp.

LOCALITIES AND MATERIAL. Fragments probably of this genus have been found at Foxhole Coppice, Monkhopton (25 ft. below "*Psammosteus*" Limestone) and at Targrove Dingle 6 (100 ft. below "*Psammosteus*" Limestone).

Genus ***TESSERASPIS*** Wills, 1935

Tesseraspis tessellata Wills

Tesseraspis sp.

LOCALITIES AND MATERIAL. Except at the type locality, Earnstrey Brook (Leath 3: 70 ft. below "*Psammosteus*" Limestone), the material is extremely fragmentary, although widely distributed. Specimens have been recorded from the following localities:

Abdon Bridge (140 ft. above "*Psammosteus*" Limestone); Clapgate Cottage Quarry (110 ft. above "*Psammosteus*" Limestone); ? Heath Quarry (300 ft. above "*Psammosteus*" Limestone); Hudwick Dingle 1 (immediately above "*Psammosteus*" Limestone); ? Kidnall Gutter 4 (200 ft. above "*Psammosteus*" Limestone); Little Oxenbold (50 ft. below "*Psammosteus*" Limestone); New Inn 1 (16 ft. below "*Psammosteus*" Limestone); Oak Dingle (125 ft. above "*Psammosteus*" Limestone); Park Barn Quarry (80 ft. above "*Psammosteus*" Limestone); Parlour Coppice (400 ft. above "*Psammosteus*" Limestone); ? Silvington, Waterfall (600 ft. above "*Psammosteus*" Limestone).

The range is from 50 ft. below the "*Psammosteus*" Limestone to 400 ft. (? 600 ft.) above it, the higher records being based on uncertain fragments, possibly in some cases of *Weigeltaspis*.

Genus ***CORVASPIS*** A. S. Woodward, 1934

Corvaspis kingi A. S. Woodward

LOCALITIES AND MATERIAL. Apart from the type-locality, Earnstrey Brook (Leath 3: 70 ft. below "*Psammosteus*" Limestone), the material is very fragmentary. Single fragments of this or a related species have been found at Hudwick Dingle 1 (immediately above "*Psammosteus*" Limestone) and Little Oxenbold (50 ft. below "*Psammosteus*" Limestone). A doubtful specimen is recorded from Jubilee Brook (250 ft. above "*Psammosteus*" Limestone).

The range of this species is from 70 ft. below to ? 250 ft. above the "*Psammosteus*" Limestone.

Genus ***ANGLASPIS*** Jaekel, 1927

Anglaspis macculloughi (A. S. Woodward)

LOCALITIES AND MATERIAL. The only extensive material comes from Earnstrey Brook (Leath 3: 70 ft. below "*Psammosteus*" Limestone), where it is very fine and plentiful, but rare and fragmentary specimens from the following places are almost certainly conspecific: Clapgate Cottage Quarry (110 ft. above "*Psammosteus*" Limestone); Clee St. Margaret (675 ft. above "*Psammosteus*" Limestone); Hudwick Dingle 1 (immediately above "*Psammosteus*" Limestone); Little Oxenbold (50 ft. below "*Psammosteus*" Limestone); Targrove Dingle 1 (18 ft. above "*Psammosteus*" Limestone); New Buildings E/3 (75 ft. below "*Psammosteus*" Limestone); New Inn 2 (75 ft. above "*Psammosteus*" Limestone).

The range of this species in this area is therefore from 75 ft. below to 675 ft above the "*Psammosteus*" Limestone.

Genus ***PORASPIS*** Kiaer, 1930

Poraspis sp.

LOCALITIES AND MATERIAL. All the specimens are small rare fragments of shields. Specimens are recorded from Aston Hill Wood 2 (relationship to "*Psammosteus*" Limestone unknown); Bromdon Dingle Brook (Lower Dittonian); Jubilee Brook 1 (250 ft. above "*Psammosteus*" Limestone); Lye Brook 4 (75 ft. above "*Psammosteus*" Limestone); New Inn 1 (16 ft. below "*Psammosteus*" Limestone); New Inn 2 (75 ft. above "*Psammosteus*" Limestone).

Therefore the local range is from 16 ft. below to 250 ft. above the "*Psammosteus*" Limestone.

Genus ***TRAQUAIRASPIS*** Kiaer, 1932

Traquairaspis symondsi (Lankester)

LOCALITIES AND MATERIAL. Apart from the classical locality of Earnstrey Brook (Leath 3: 70 ft. below "*Psammosteus*" Limestone), about 30 good fragments and a fine dorsal disk (P.31146) from Lye Brook 1 (125 ft. below "*Psammosteus*" Limestone) ; a good ventral plate (P.34345) from Lye Brook 3 (90 ft. below " *Psammosteus* " Limestone) and another (P.30026) from Little Oxenbold (50 ft. below " *Psammosteus* " Limestone), the material consists of small rare fragments : Clapgate Cottage Quarry (110 ft. above " *Psammosteus* " Limestone) ; Hudwick Dingle 1 (immediately above " *Psammosteus* " Limestone) ; Kidnall Gutter 1A (30 ft. above " *Psammosteus* " Limestone) ; Lye Brook 1 (125 ft. below " *Psammosteus* " Limestone) ; New Buildings E/3 (75 ft. below " *Psammosteus* " Limestone) ; New Inn 1 (16 ft. below " *Psammosteus* " Limestone) ; Oak Dingle (125 ft. above " *Psammosteus* " Limestone) ; Sudford Dingle 1 (3 to 4 ft. above " *Psammosteus* " Limestone) ; Targrove Quarry (175 ft. above " *Psammosteus* " Limestone).

The total range in the area is from 125 ft. below to 175 ft. above the " *Psammosteus* " Limestone, but apart from that from Hudwick Dingle 1 and Sudford Dingle 1, where the fossiliferous beds lie just over the " *Psammosteus* " Limestone, the total material from above the " *Psammosteus* " Limestone consists of ten very small fragments ; three from Clapgate Cottage Quarry (110 ft. above) ; one from Oak Dingle (125 ft. above) and six from Targrove Quarry (175 ft. above).

Genus ***PTERASPIS*** Kner, 1847

Subgenus ***PTERASPIS*** typicum

Pteraspis (Pteraspis) rostrata (Agassiz)

LOCALITIES AND MATERIAL. The surviving type-specimen (Agassiz, 1935 : 148, pl. 1*b*, fig. 6) is a small unsatisfactory specimen, 5·2 cm. long as preserved, largely an internal cast. Only the base of the snout is preserved as an impression, and this and the form of the cornua establish the species, but not the variety. The specimen came from Whitbatch, Shropshire, a locality in which several quarries were worked from time to time (about 200 ft. above the " *Psammosteus* " Limestone), and from this area material of *Pteraspis* is rare and *Cephalaspis* is relatively common. The *Pteraspis* material comprises ventral disks 6–7 cm. long (P.43448–51) and an even larger fragment (P.43453), and the posterior end of a shield ; but none is sufficient to indicate the particular form, even if such indirect argument were in the circumstances acceptable.

Only nine or ten other localities in the Clee area have produced rostra to establish the occurrence of the species, and in two cases these are unusually broad. Doubtless much of the material identified merely as *Pteraspis* sp. belongs to *P. rostrata.* Specimens assigned to undetermined forms in addition to those from Whitbach are :

Hudwick Dingle 4. Three rostra and a fragment (175 ft. above " *Psammosteus* " Limestone).

Kidnall Gutter 1. A rostrum (P.34328) and a ridge-scale (P.34327). The rostrum is exceptionally broad. (15 ft. above " *Psammosteus* " Limestone.)

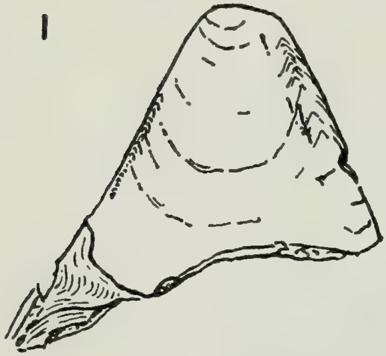
New Buildings E/2. One very broad rostrum (P.34336) which is not, however, very different from a diseased specimen from Guildings Brook (P.16472). (110 ft. above " *Psammosteus* " Limestone.)

Rea Bridge, Ditton Priors. Good rostrum (P.31640). (Not *in situ.*)

Pteraspis (Pteraspis) rostrata var. ***waynensis*** White

(Text-fig. 1)

Jubilee Brook 1. Two rostra with part of orbitals, etc. attached (P.30053, P.30056). The inner anterior borders of the orbitals are concave and the medial extensions meet the pineal plate. The second specimen is 2·7 cm. in length with a maximum breadth of 2·4 cm. (Text-fig. 1). (250 ft. above "*Psammosteus*" Limestone.)



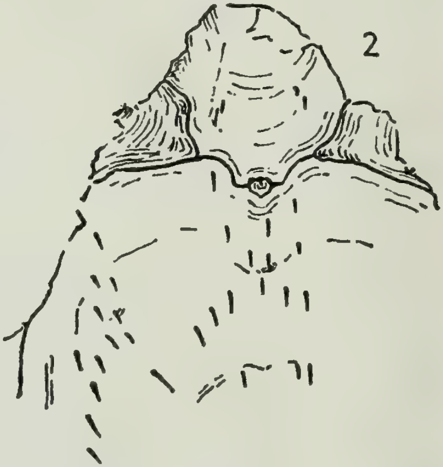


FIG. 1. *Pteraspis* (*Pteraspis*) *rostrata* var. *waynensis* White. Rostrum with part of left orbital plate. Jubilee Brook 1. P.30056. × 1·5.

FIG. 2. *Pteraspis* (*Pteraspis*) *rostrata* var. *trimpleyensis* White. Anterior part of dorsal shield, in impression. Bouldon Ford. P.29955. × 1·5.

Pteraspis (Pteraspis) rostrata var. ***trimpleyensis*** White

(Pl. 34, fig. 5 ; Pl. 35, figs. 1, 2 ; Text-fig. 2)

Bouldon Ford. External impression of part of dorsal shield with abnormal sensory canals (P.29955 ; Text-fig. 2) and other fragments. (50 ft. above "*Psammosteus*" Limestone.)

Oak Dingle. Right half of small dorsal disk (P.33573–74 ; Pl. 35, fig. 2), rostrum with parts of orbitals (P.33572) and other fragments. (125 ft. above "*Psammosteus*" Limestone.)

Ledwyche Brook. Anterior part of dorsal shield with rather short and broad rostrum, 2 × 1·8 cm. (P.33766 ; Pl. 35, fig. 1). (50 ft. above "*Psammosteus*" Limestone.)

Targrove Quarry. Greater part of old dorsal shield (45963) and several fragments almost certainly of this form. (175 ft. above "*Psammosteus*" Limestone.)

Remarks. The ranges shown are as follows :

Pteraspis (*P.*) *rostrata* var. indet. . .	15–200 ft. above " *Psammosteus* " Limestone.
Pteraspis (*P.*) *rostrata* var. *waynensis* .	250 ft. above " *Psammosteus* " Limestone.
Pteraspis (*P.*) *rostrata* var. *trimpleyensis* .	50–175 ft. above " *Psammosteus* " Limestone.

Pteraspis (Pteraspis) dairydinglensis sp. nov.

(Pl. 33 ; Pl. 34, figs. 1–4 ; Pl. 35, figs. 4, 5 ; Pls. 37–41 ; Text-figs. 3–5)

Diagnosis. A typical *Pteraspis* with dorsal shield (without spine) attaining a length of 10 cm., strongly vaulted, with maximum breadth of disk when flattened about four-fifths of its total length ; anterior margin of disk with wide, shallow median indentation and usually rounded antero-lateral corners ; posterior margins long and gently concave when uncrushed ; spinal socket about one-third of total length of disk and two-thirds of short compressed triangular spine. Rostrum very short with somewhat angular tip, its length being about one-quarter of the total length of the dorsal shield (without spine) and four-fifths of the distance between the orbital openings. Pre-oral field very short. Pineal plate much wider than long, moderately large and meeting medial extensions of orbital plates except superficially in some old specimens. Branchial plates wide and longitudinally keeled, the flat or slightly concave upper and lower surfaces divided by an acute angle of about 65°. Cornual plates rather narrow, reaching level of centre of ossification of dorsal disk, with concave posterior margin or short hook when abraded.

Ventral disk of usual ovoid shape, much vaulted with rounded or briefly flattened anterior margin and obtuse posterior angle partly overlapped by first ventral ridge-scale.

Ridges of ornamentation ± 60 per cm., gently rounded in section when fresh. Ornamentation on scales consisting of longitudinal ridges divided by chevron-shaped grooves at intervals slightly increasing to rear, rarely with anterior ridges parallel with front margin.

Holotype. Imperfect dorsal shield (P.29936 ; Text-fig. 3).

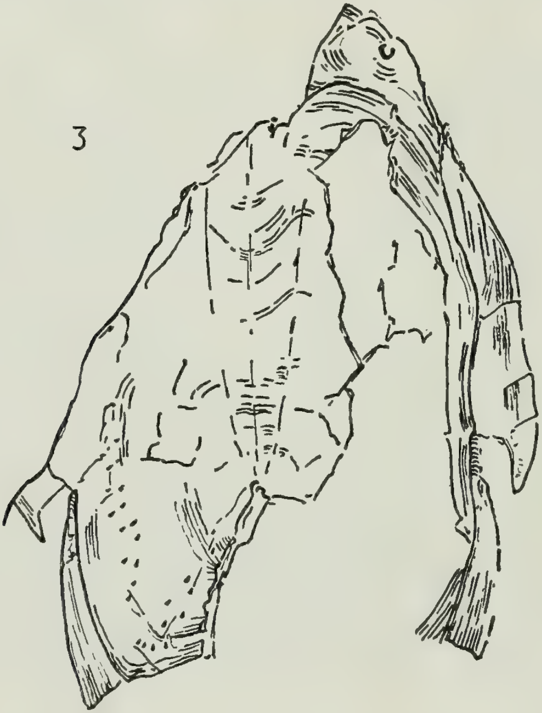
Material. The material is extensive but although mostly fragmentary is well preserved. In addition to the holotype it includes half-a-dozen imperfect dorsal shields, five ventral disks, a dozen rostra, over 50 other substantial fragments of various parts including a number of oral and circum-oral plates, and more than 100 isolated scales.

Localities. Bulk of material from Dairy Dingle, East of Neenton ; also from Derrington Rea Bridge, North of Ditton Priors, and a few pieces and scales, almost certainly of this species, from Upton Cresset. The most complete shields come from the Hopton Brook section near Hopton Wafers, and a snout from Hazeley Brook West, outside the area studied.

The position of the Clee localities are: Dairy Dingle (800 ft. above "*Psammosteus*" Limestone); Derrington Rea Bridge (500 ft. above "*Psammosteus*" Limestone); Upton Cresset (400 ft. above "*Psammosteus*" Limestone).

DESCRIPTION. The dorsal shield (P.42366, Pl. 33, fig. 2) from Hopton Brook is by far the most complete specimen and lacks only the left anterior region. Like all the other dorsal shields it is partly flattened and so appears considerably broader than in life. The region around the socket of the dorsal spine is naturally thick and thus reinforced does not crush so readily and still retains much of its original shape, whereas the rostrum is flattened. As preserved the total length, including the socket, is 9·3 cm., the breadth 6·2 cm. flat at the maximum (just in front of the branchial opening) and about 7·2 cm. over the curve.

3



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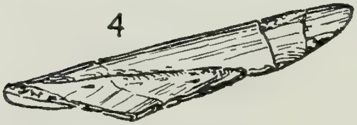


Pteraspis (*Pteraspis*) *dairydinglensis* sp. nov.

FIG. 3. Imperfect dorsal shield. The holotype. Dairy Dingle. P.29936. × 1·2.
FIG. 4. Dorsal spine. Derrington Rea Bridge. P.42005. × 1·6.

In this specimen the rostrum is short and is a little less than one-quarter of the length of the shield. It usually appears to be very broad owing to flattening (Pl. 34, figs. 1, 3; Text-fig. 6), and the measurements in various specimens are:

Specimen	Locality	Length (cm.)	Max. breadth over curve (cm.)
P.42366	Hopton Brook	2·3	3·4*
P.42361	,,	2·5	3·2
P.42360	,,	2·0	3·2
P.32249	Derrington	1·9	2·6
P.32248	,,	2·5	3·1
P.29997	Dairy Dingle	2·0	3·0*

* Double half breadth.

The real form of this plate, which is quite high, is only seen in P.42360 of which the maximum breadth when viewed directly is 2·7 cm., 0·5 cm. less than over the curve (Pl. 33, fig. 1).

Isolated rostra or fragments of them are exceptionally common, especially the solid tips, for there is usually a large space above the pre-oral field occupied in life by cartilage. The undersurface of the snout is very like that of *P. rostrata* (Pl. 34, figs. 1*a*, 5), only much shorter, especially in the younger specimens, in one of which (Pl. 34, fig. 2) a very marked median spur is preserved.

There are twelve isolated oral or tooth-plates excellently preserved (P.43709–20; Pl. 37). As in *P. rostrata* (White, 1935 : 408, text-figs. 41–47) they are flat and wide proximally, high and narrow distally.

The median oral plate (or plates) is very short and cut off from the post-oral covers by those on either side (Pl. 37, fig. 1). It consists chiefly of the large head, resembling a triangular arrow-head, which greatly overhangs the smooth inner surface. The neighbouring tooth-plates are longer and curved, but the plates increase in length and become straighter towards the corners of the mouth, and at the same time the heads become smaller. The outer or lower surface is ornamented, so are all the sides of the heads (cf. Stensiö, 1958 : 265). The plates overlapped one another decreasingly outwards, the area of overlap being wide in the middle of the series, but at the sides the lateral face on the outermost plate has an almost vertical contact with the fixed lateral oral plate. All but the short median plate were overlapped proximally by the post-oral covers, and the inner surface, by which each plate was doubtless attached to a cartilaginous framework, is smooth except for a few pores.

The ornamentation of the heads of these plates consists of numerous slightly raised triangles, none of which shows any sign of wear. On the outer surface the dentine ridges are short and transverse, with occasionally a few longitudinal ridges along the overlapped margin. Ventrally the ornament sometimes shows signs of having been rubbed by movement against the post-oral covers (Pl. 37, fig. 10). The smooth basal layer of the inner surface is thin and shows a number of openings for vascular canals.

A careful re-examination of the oral plates of *P. rostrata toombsi* (White, 1935 : 408, text-figs. 41–48) shows that they are in fact similar in shape and disposition to those described here. Neither in that form nor in *P. dairydinglensis* are there any signs of the false upper dentures with which Stensiö (1958 : 350, text-figs. 191A, B, etc.) has invested the pteraspids, and their supposed presence is against all the evidence. In the former species where the plates are all preserved in place as moulds such a feature would certainly be apparent and in the case of the new species, where very delicate plates are preserved as complete entities there is no sign of them ; moreover the tips of the dental plates show no signs whatever of wear, as would be bound to appear if they worked against an upper set. They must have had some degree of movement or the mouth could have opened but relatively little, possibly no more than the areas of overlap indicate ; and since these are unilateral towards the outside, with the largest in the middle and below, the movement must have been towards forming a scoop, that is with the centre pushed forwards relatively to the sides. *Pteraspis* probably fed on organic matter off the bottom in muddy waters, as already suggested (White, 1935 : 412), but the vaulted ventral and dorsal plates clearly indicate that they were free swimming, as the hypocercal tail also shows (Kermack 1943), although not very efficiently so. It is possible that the more strongly vaulted forms such as *P. dairydinglensis* were also surface-feeders, as Harris (1936) has suggested in the case of the more evenly balanced Anaspids. Such forms, which usually appear to be wider and flatter than the others owing to crushing, always have short snouts and therefore small pre-oral fields, and since these are sensory areas connected with food-finding, it is probable that their restriction in size does go with surface-feeding where feeding would be more nearly mechanical or based partly on sight, and where a relatively broader mouth would be useful. The long, broad-snouted pteraspids, like *P.* (*Cymripteraspis*) *leachi* and *P.* (*Rhinopteraspis*) *dunensis*, usually large animals with even smaller pre-oral fields were possibly also surface—or even mid-water feeders living in stronger currents, sometimes under estuarine conditions, but *P.* (*Belgicaspis*) *crouchi* with a narrow typically rounded snout and large pre-oral field was probably again a bottom-feeder in cloudy water, as its frequent association with *P.* (*P.*) *rostrata* indicates. It is perhaps not without significance that only once has *P.* (*P.*) *dairydinglensis* been found with another species, *P.* (*B.*) *crouchi*, and it is possible that the appearance of broad, long-snouted forms in the higher beds is connected with changed environmental conditions. It seems likely that the extreme rarity of pteraspids in the Scotch Lower Old Red Sandstone is due to the lacustrine conditions there prevalent, for these would be less suitable for free-swimming forms like pteraspids with their ability, albeit limited, to live in current-dominated areas, such as rivers and estuaries, than for the wholly bottom-dwelling cephalaspids, whose flat underside and dorsal eyes clearly show their usual method of living on the bottom, preferably of quiet waters.

The dorsal disk has the usual outline, heart-shaped in front and pointed behind. The anterior indentation is wide to accommodate the short, wide pineal plate, and the front corners are rounded. The median length (including spinal socket) of the most complete specimen (Pl. 33, fig. 1) is 6·9 cm., the maximum breadth over the curve, 6 cm. The hinder part of the plate is much vaulted (Pl. 33, fig. 3) and the hinder margin on each side of the spine was in life nearly straight.

The dorsal spine was clearly short and deep (Text-fig. 4; P.32243) but although the specimen figured has little missing, the tip is rubbed and may have been somewhat more pointed.

The orbitals are rather short but wide, with their medial extensions usually in full contact with the very wide and short pineal plate (Pl. 33, figs. 1, 2; Pl. 34, figs. 1, 3, 4).

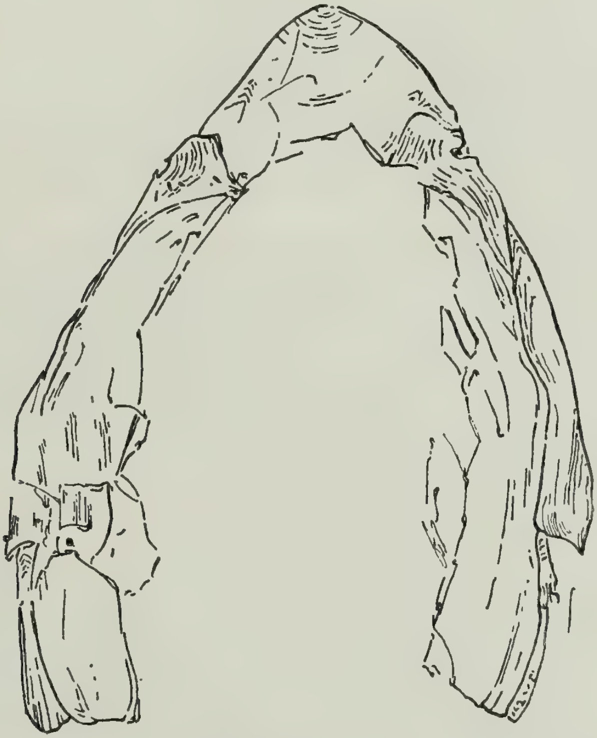


Fig. 5. *Pteraspis* (*Pteraspis*) *dairydinglensis* sp. nov. Imperfect dorsal shield. Hopton Brook 4. P.42364. × 1·2.

The branchial opening is at about two-thirds of the distance from the anterior margin to the posterior outer corner of the disk, so that the branchial plates are relatively long (Pl. 33, fig. 1). The plates have a very marked keel dividing the almost flat upper and lower surfaces (Pl. 33, figs. 4, 4*a*) which are separated by about 65°. The cornual plate is narrow but increases in width to the rear, ending in a slight flat hook, which is usually rubbed off (Pl. 33, figs. 2, 4, 5).

The ventral disks (Pl. 35, figs. 4, 5) show no special features. They were undoubtedly very convex in life, like the dorsal shield, and consequently appear short and broad when flattened. The transverse front margin is very short and the posterior point blunt with its two sides slightly concave.

Owing to the nature of the matrix, which disintegrates in acetic acid, a very large number of isolated scales were obtained (Pl. 39, figs. 9–25; Pls. 40, 41). Their variation in shape, size and function conforms to the usual pattern in *Pteraspis* (see White, 1935 : 414, 419, pl. 27, text-figs. 51–65; 1950 : 81, text-figs. 10–13) with the several kinds of ridge-scales, flank-scales, double flank-scales and so on. One point not previously observed is the piercing of scales for the continuation of the sensory canals from the carapace on to the hinder part of the body; this can be seen in some seventeen specimens (Pl. 39, figs. 9–25). The canal entered the scale in the anterior overlapped area and left it in the short overlapping margin on the inner surface some distance from the hinder margin. There was no external opening through the scale. This explains why indications of the lateral lines are so rare, even in the complete specimens with tails, which are preserved as external impressions. In these only one shows substantial parts of this system on the squamation, parts of both left and right dorsal lines appearing as infillings of the canals (White, 1935 : 42, text-fig. 64).

There were three pairs of lateral lines, as the dorsal and ventral disks show, a dorsal line on each side of the dorsal ridge-scales, the main dorsal lateral line running low on the upper surface just above the level of the cornua, and a ventro-lateral line just below the level of the cornua and branchial plates. Of the extent of these lines we only know that the dorsal line ran almost to the caudal constriction at least. It is difficult to ascertain to which of these lines the isolated scales belong, in particular, as between the two lateral canals, but the smaller scales, especially the more oblique ones, probably belong to the dorsal line. Nor can one be certain of the distribution of all the ridge-scales. The long scales with little anterior overlap are almost certainly dorsal ridge-scales from the separated anterior series, while the more compressed scale (No. 32) is from the pre-caudal row. The broad flattish scales (P.43621–23) are ventrals, and so are the two very different simply ornamented scales (Pl. 40, figs. 10, 11) characteristic of the anterior ventral ridge- series.

The predominantly diamond-shaped body-scales show a remarkable range in form, and include the usual double scales (Pl. 40, figs. 14–27; Pl. 41).

The ornamentation of the scales is typical of the genus, but varied in detail. In general it resembles that of *P.* (*P.*) *rostrata trimpleyensis*, without anterior ridges parallel with the front margin, and with the chevron-grooves more or less evenly distributed on the body of the scales, except on the ridge-scales. On the anterior ventral ridge-scale they are entirely absent, and on the others the intervals separating them increase rapidly towards the rear. There are, however, a number of flank scales in which the anterior ridges appear in varying numbers and in some they are as numerous as in those of the typical scales of *P.* (*P.*) *rostrata toombsi* (White, 1935, pl. 27). The area of overlap is variable but usually narrow.

A curious feature of these scales in general is the frequency with which the ornamentation is carried over on to the underside at the free posterior end. It suggests that there were considerable pockets of epidermis and that the scales did not lie flat but were raised like spent pine-cones. This is also shown in the American *P. carmani* (Denison, 1960 : 396, fig. 141J) and is probably common to all species.

Like the scales and oral plates, a number of circum-oral plates have been isolated from the matrix, all but one from Dairy Dingle (Pl. 38; Pl. 39, figs. 1–8).

There are five examples of anterior lateral plates (Pl. 38, figs. 4, 5). They are distinguished at once by the branched sensory canal system which consists of a large, short canal near one side with a single smaller branch nearly at right angles to it. The main canal is a segment of the ventral longitudinal canal which runs from the ventral disk through the lateral plates on to the dorsal side of the snout. The plates are wider than long, the smaller one figured being irregularly squarish, the larger almost L-shaped. These two are clearly from opposite sides of the animal, and both show an overlapped projection to one side. The smaller lateral canal opens towards the curved longer margin which is feather-edged with the ornament invading the undersurface. Clearly this must be the free side along the ventral disk and thus, the overlapped projection must be for the fixed lateral oral plate which itself is overlapped along the rest of the contact. There is no branch in this plate to the orbital behind the orbit, so that the infraorbital sensory canal must have been discontinuous.

Four out of seven posterior lateral plates are figured (Pl. 39, figs. 1–4). They are in general considerably longer than wide with the sides roughly parallel. Their distinguishing feature is the single sensory canal, which runs down their length, usually forming a broad ridge on the undersurface. Like all these circum-oral plates, the shape is varied and they tend to fuse to the sides of the shield. One such plate shows that the basal and polygonal layers were completely fused to the shield, but that the outer layer was free (cf. White, 1938, text-figs. 2–4).

The nine fixed lateral oral plates (Pl. 38, figs. 1–3) are roughly triangular, sometimes with the apex truncated, in which case there will have been a smaller triangular plate such as in *P.* (*P.*) *rostrata toombsi* (White, 1935, text-figs. 43, 45). The single canal crosses the plate but probably missed the small anterior plate when separate. The contacts of the larger plate are deep and nearly vertical. This plate sometimes fuses to the oral margin of the rostrum forming a marked " angle préorogoniale " (Pl. 34, fig. 1*a*) such as is said to characterize certain of Stensiö's (1958, text-fig. 139, etc.) forms.

The post-oral covers (Pl. 39, figs. 5–8) are amazingly variable in shape, and the number also must have been variable in order to accommodate such odd shapes, most of which show overlapping sides. All are marked by concentric ornamentation and the absence of sensory canals.

It is interesting to note that none of the lateral plates nor the post-oral covers shows any sign of internal ornamentation other than occasionally at the margin, as in some scales. This is in contrast to the condition described by Stensiö (1958 : 265, text-figs. 140B, 191A, B) on which he bases the presence of his " fente post-orogoniale ".

REMARKS. *P.* (*P.*) *dairydinglensis* in all its known features is just an exaggerated, vaulted, short-snouted edition of *P.* (*P.*) *rostrata* from which it was undoubtedly derived. Isolated fragments of plates or isolated scales would often be difficult or impossible to identify with one species or the other, and this provides a warning in accepting past identifications based on such material.

The vaulted shape, as noted above, suggests that this species may have been a freer swimmer than *P.* (*P.*) *rostrata* and a surface rather than a bottom-feeder.

The range of *P.* (*P.*) *dairydinglensis* is 400 to 800 ft. above the "*Psammosteus*" Limestone; approximating to the upper part of the *crouchi* Zone.

Subgenus ***BELGICASPIS*** Zych, 1931

Pteraspis (Belgicaspis) crouchi Lankester

(Pl. 36, figs. 2–11)

LOCALITIES AND MATERIAL.

Batch Brook. Small imperfect dorsal disk, 3·1 cm. long and about 2 cm. broad, with large pineal indentation (P.33799). Near var. *heightingtonensis*. (800 ft. above "*Psammosteus*" Limestone.)

Clee St. Margaret. Numerous pieces, chiefly fragments. One narrow dorsal disk 4·2 cm. long and 2·4 cm. broad (P.32171). Near var. *heightingtonensis*, but sides not so straight as in holotype. There are seven remarkable rostra, all short and triangular (e.g. P.29833–35, P.32164–66, P.32179; Pl. 36, figs. 6–8). (675 ft. above "*Psammosteus*" Limestone.)

Earnstrey Hall 1. Several fragments including good small normal rostrum and a dorsal spine (P.27067–68) and a normal small rostrum and one broader on same slab (Pl. 36, figs. 4, 5), the measurements being 1·3 × 0·35 cm. and 1·5 × 0·6 cm. respectively. (400 ft. above "*Psammosteus*" limestone.)

Earnstrey Hall 2. Fragment probably of this species. (420 ft. above "*Psammosteus*" Limestone.)

Great Northwood. Fragment probably of this species. (Upper part of lower group.)

Heath Quarry. Small typical rostrum; a very imperfect dorsal disk over 5·5 cm. long and 4·0 cm. wide (P.29847); a good branchial (Pl. 36, fig. 2) about 4·5 cm. long when complete with the undersurface having a maximum breadth of 0·9 cm.; and other fragments. (300 ft. above "*Psammosteus*" Limestone.)

The Hills, Downton. Isolated typical rostrum, and dorsal and ventral disks. (Position uncertain.)

Kidnall Gutter 3. A typical branchial (P.43222) and other fragments. (About 180 ft. above "*Psammosteus*" Limestone.)

Middleton Priors. Six rostra, one ventral disk 7·6 cm. long, etc. (500 ft. above "*Psammosteus*" Limestone.)

New Buildings B. One large dorsal disk 5·5 cm. long and about 4 cm. wide. (Loose block.)

Oldfield, the Lobby. Rostrum etc. (Position uncertain.)

Silvington, Drainage Gully. Typical pieces of disk. (575 ft. above "*Psammosteus*" Limestone.)

Silvington, Waterfall. Very numerous specimens. The dorsal disks range in size from 5·5 × 3·6 cm. (P.29877) through 4·0 × 2·6 cm. (P.29045) down to 2·8 × 2 cm. (P.29881), approaching var. *heightingtonensis* in form. The rostra show a remarkable range in size and shape (Pl. 36, figs. 9–11), the largest

(P.29043) is normal in shape, the middle sizes are triangular (P.29832, P.29041, P.29830) and the smallest are a little longer than wide (P.29823–24, P.29831, P.29042). (About 600 ft. above " *Psammosteus* " Limestone.)

Sudford Dingle 2. Small narrow rostrum (P.34332) and other fragments. (About 170 ft. above " *Psammosteus* " Limestone.)

Targrove Dingle 3. Part of large narrow rostrum (P.43023), etc. (About 250 ft. above " *Psammosteus* " Limestone.)

Remarks. The known range of this species is very different from that of *P.* (*P.*) *rostrata*, starting at about 170 ft. above the " *Psammosteus* " Limestone it reaches 800 ft., so that in this area, the two species only overlap at the very bottom of its range; but in fact they have never been taken together in the Clee district, although they certainly occur together elsewhere.

The most interesting feature of this species is the occurrence of very short rostra in several localities. They undoubtedly belong to *P.* (*B.*) *crouchi* and are usually associated with others of normal shape. They all show the single cross-over of the ridges of the ornamentation from the upper to the lower surface typical of this species, which clearly distinguishes them from rostra of nearly similar shape of *P.* (*P.*) *rostrata*. In the latter the ridges form a Z-pattern along the sides (cf. Pl. 35, fig. 1 and Pl. 36, figs. 6–11).

These rostra cannot represent growth-stages, for some of the short and long rostra belonged to animals of comparable size (Pl. 36, figs. 4, 5), and in any case, one rostrum could not develop from another except by complete resorption, of which I have seen no evidence. It is also unlikely that they represent sexual dimorphism, although a similar phenomenon is known in *P.* (*P.*) *rostrata*, for there is considerable variation in the form of the short snouts and there may be gradations between the two types.

The explanation of the phenomenon is probably quite different. *P.* (*B.*) *crouchi* is a very specialized isolated form, particularly in respect of its snout. When typically developed it is unlike that of any other species of *Pteraspis*. The rostrum of *Pteraspis* in the earlier forms, was short and broad, and among such were the ancestors of *P.* (*B.*) *crouchi*. It is probable that the spasmodic occurrence of these unusual stout and broad snouts both in this species and in *P.* (*P.*) *rostrata* is due to a degree of 'atavism' (de Beer, 1951: 104), possibly brought about by genetic drift in small, relatively isolated populations.

The short snouts have not been found below 400 ft. above the " *Psammosteus* " Limestone, but the amount of material in the lower beds is not significant.

Subgenus ***SIMOPTERASPIS*** White, 1950

This subgenus was founded on *P. leathensis* White (1950 : 76) and also was held to include *P. gosseleti* Leriche, *P. primaeva* Kiaer and *P. vogti* Kiaer, all small short-snouted forms. Of these only in *P. leathensis* (Pl. 35, fig. 3*a*) and *P. primaeva* is the important pre-oral region known and thus the relationships of *P. leathensis* to *P. gosseleti* which Leriche (1924 : 149, footnote) has made the type a subgenus of

Protopteraspis on the supposition that the spine was not separated from the dorsal disk, is uncertain and they are for the time being retained in the subgenera of which they are the respective types.

Pteraspis (Simopteraspis) leathensis White

(Pl. 35, figs. 3, 3*a*)

Localities and material. This species is recorded from eleven localities.

Aston Hill Wood 1. External impression of whole dorsal shield and spine (P.25253). (Loose blocks from unknown level.)

Clapgate Cottage Quarry. Fragment possibly referable to this species (P.37776). (110 ft. above "*Psammosteus*" Limestone.)

Hudwick Dingle 1. Poor fragments, probably of this species. (Immediately overlying "*Psammosteus*" Limestone.)

Hudwick Dingle 3. External impression of anterior half of large dorsal shield (P.42834–35), ventral disk (P.34042), etc. (80 ft. above "*Psammosteus*" Limestone.)

Kidnall Gutter 1A. Typical fragments including part of rostrum (P.43109) and disk (P.43110). (30 ft. above "*Psammosteus*" Limestone.)

Leath 1. The type locality. (Level unknown, but ?Ditton Series, lower group).

Lye Brook 2. Fragments probably of this species. (Position uncertain.)

Lye Brook 4. Imperfect dorsal shield (P.26927), etc. (75 ft. above "*Psammosteus*" Limestone.)

New Inn 1. Over 40 specimens finely preserved, mostly fragmentary, but including fine dorsal shields (P.34120, Pl. 35, fig. 3; P.34076), dorsal spine (P.34256) and ventral disks (P.34851). (16 ft. below "*Psammosteus*" Limestone.)

New Inn 2. A dozen finely preserved typical fragments and scales (P.34518–27, P.43014, (75 ft. above "*Psammosteus*" Limestone.)

Yewtree Dingle. Characteristic ventral disks (e.g. P.26937–38); rostrum (P.26942) and other fragments. (50 ft. above "*Psammosteus*" Limestone.)

Remarks. *P.* (*S.*) *leathensis* ranges from 16 ft. below to 110 ft. above the "*Psammosteus*" Limestone.

Order ANASPIDA

A single scale (P.28665) is recorded from Targrove Dingle 6 (100 ft. below "*Psammosteus*" Limestone).

Order THELODONTI

Thelodont scales have been noted from about 20 localities in the lower group, ranging from Lye Brook 3 (90 ft. below the "*Psammosteus*" Limestone) to Batch Brook and Dairy Dingle (800 ft. above). Almost invariably they are accompanied by Acanthodian scales. It is probable that their presence is universal, and the restricting factor is the ease with which the matrix yields to acid treatment. At the moment insufficient material has been recovered to make a close study worth while.

Order OSTEOSTRACI

Genus ***CEPHALASPIS*** Agassiz, 1835

Cephalaspis acutirostris Stensiö

LOCALITY. Whitbatch Quarry (about 200 ft. above "*Psammosteus*" Limestone).

Cephalaspis cf. ***agassizi*** (Lankester)

LOCALITY. Bluck's House (Ditton Series, lower group), centre of shield (P.33752).

Cephalaspis cf. ***fletti*** Stensiö

LOCALITY. Bluck's House (Ditton Series, lower group), centre of shield (P.33749–50).

Cephalaspis cf. ***langi*** Stensiö

LOCALITY. Bluck's House (Ditton Series, lower group), a small badly preserved head shield (P.33751) measuring 3·7 cm. across base of cornua, with rounded rostral margin.

Cephalaspis lankesteri Stensiö

LOCALITY. Whitbatch Quarry (about 200 ft. above "*Psammosteus*" Limestone).

Cephalaspis whitbatchensis Stensiö

LOCALITY. Whitbatch Quarry (about 200 ft. above "*Psammosteus*" Limestone).

Cephalaspis whitei Stensiö

LOCALITY. Whitbatch Quarry (about 200 ft. above "*Psammosteus*" Limestone).

Cephalaspis bouldonensis sp. nov.

(Pl. 36, fig. 1; Text-fig. 6)

DIAGNOSIS. A *Cephalaspis* of moderate size, with maximum breadth of cephalic shield across top of pectoral sinuses, approx. 7 cm. when complete, and probably about one and one-third times median length. Rostral margin broad and rounded, the shield being semicircular. Length of cornua not known; pectoral sinuses wide and shallow. Interzonal part short, broad and high. Orbital openings small in middle of length of cephalic shield. Dorsal sensory field, bottle-shaped, two and one-third times as long as broad at the maximum. Lateral sensory fields reaching backwards on to cornua.

Holotype. Imperfect cephalic shield in part counterpart (P.43055).

Locality. Bouldon Ford (about 50 ft. above "*Psammosteus*" Limestone).

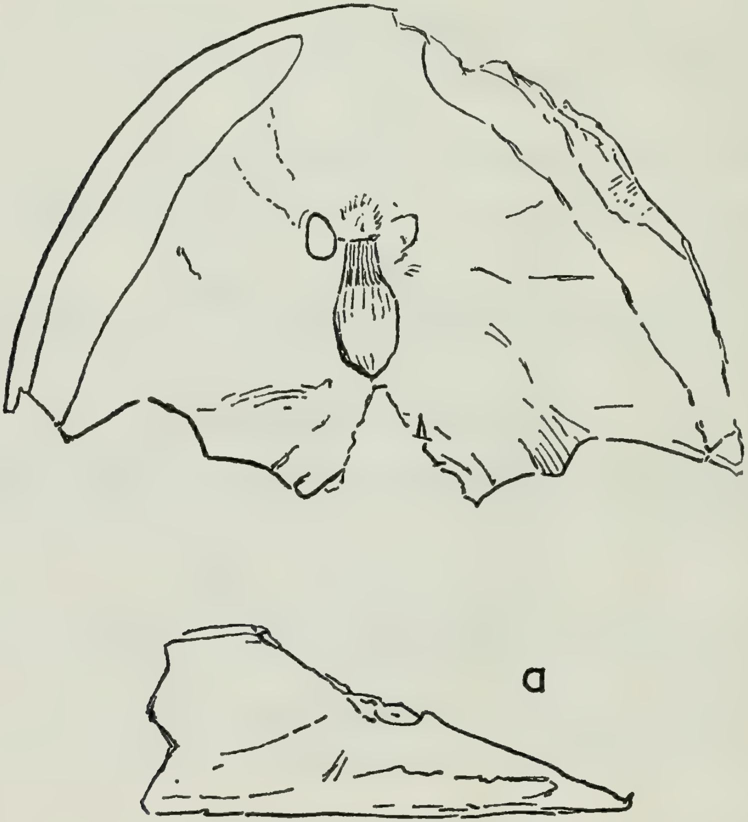


Fig. 6. *Cephalaspis bouldonensis* sp. nov. Imperfect cephalic shield partly restored from counterpart. (a) right side view. See also Pl. 36, fig. 1. The holotype. Bouldon Ford. P.43054–55. × 1·5.

Description. This specimen is in many respects badly preserved, but sufficient is present to show its unique character. The exoskeleton is thin and in poor condition, the greater part of the cornua and the middle of the interzonal part are missing, the right margin defective and the whole somewhat distorted. The shape of the shield is remarkable, for the front margin is completely rounded, and indeed the whole forms a semicircle with the centre just behind the posterior end of the dorsal sensory field. The maximum breadth across the pectoral sinuses (making allowance for the defective right side) is 7 cm. and the length, as preserved, is 4·5 cm.; the height at the back of the shield without the spine (which was certainly present) is 1·3 cm. with a straight facial profile. The specimen is probably not very much crushed.

The orbits lie approximately in the middle of the known length of the shield measured to the hinder lateral margin of the interzonal part. The sinuses are very wide without an angle and shallow.

The dorsal sensory field is narrow in front and then quickly broadens, reaching its maximum breadth near the rounded posterior end.

The normal lateral sensory fields can be clearly made out and they run onto the cornua as far as these are preserved. Nothing can be seen of the ornamentation.

REMARKS. This is one of the most distinctive of the English species, by reason of its completely semicircular shape. *C. langi* Stensiö (1932 : 134), the only other completely rounded form, is not only much smaller, but its eyes are further forward and the interzonal part relatively wider.

INDETERMINABLE CEPHALASPIDS

Other remains of cephalaspids are widely spread although rare and fragmentary. Pieces of the cephalic shields or scales occur in the following localities:

Clee St. Margaret (675 ft. above "*Psammosteus*" Limestone).
Dairy Dingle (800 ft. above "*Psammosteus*" Limestone).
Derrington Rea Bridge (500 ft. above "*Psammosteus*" Limestone).
Earnstrey Brook (70 ft. below "*Psammosteus*" Limestone).
The Hills (Ditton Series, lower group).
Hudwick Dingle 1 (immediately over "*Psammosteus*" Limestone).
Hudwick Dingle 4 (175 ft. above "*Psammosteus*" Limestone).
Kidnall Gutter 1 (15 ft. above "*Psammosteus*" Limestone).
Kidnall Gutter 3 (180 ft. above "*Psammosteus*" Limestone).
Leath 1 (? Ditton Series, lower group).
Ledwyche Brook (60 ft. above "*Psammosteus*" Limestone).
Lye Brook 1 (125 ft. below "*Psammosteus*" Limestone).
Lye Brook 3 (90 ft. below "*Psammosteus*" Limestone).
New Inn 1 (16 ft. below "*Psammosteus*" Limestone).
Oak Dingle (125 ft. above "*Psammosteus*" Limestone).
Park Barn Quarry (80 ft. above "*Psammosteus*" Limestone).
Silvington, Waterfall (600 ft. above "*Psammosteus*" Limestone).
Upton Cresset Quarry (400 ft. above "*Psammosteus*" Limestone).

The range is therefore from 125 ft. below to 800 ft. above the "*Psammosteus*" Limestone.

Class GNATHOSTOMATA

Order ACANTHODII

Acanthodian scales are closely associated with thelodont scales (q.v., p. 258) in their known distribution, and the same remarks apply regarding their probable universality.

Fin-spines of several types (*Onchus*, *Climatius*, etc.) are also fairly widespread but few in number, about 35 distributed over 15 localities. All are either very fragmentary or small. Most are probably referable to acanthodians. At both the New Inn localities partly nodular spines of the type ascribed to " *Climatius* " by Gross (1947, pl. 27) have been found (P.43008–12, P.34284) and from New Inn 2 comes also some of " *Onchus* " type (P.43003–07).

In only four localities have teeth or pieces of jawbone been found. From New Inn 2 (75 ft. above the " *Psammosteus* " Limestone) come several curious " hedgehog " multiple tooth spirals (P.42991–99) similar to those described and figured by Gross (1957 ; 5, pl. 3, figs. 1–7) under the name " *Gomphodus* " from the Upper Ludlow " Beyrichienkalk ", only much larger, up to 6 mm. across without the spines ; and from New Inn 1 (16 ft. below the " *Psammosteus* " Limestone) comes an even larger example, 7 mm. across (P.34287). Still larger tooth spirals, 1 cm. across (P.29709–12) have been collected at Onen, Monmouthshire in association with *Traquairaspis symondsi*.

Genus ***ISCHNACANTHUS*** Powrie, 1864

Two fragments of acanthodian jawbone have been collected in the area, one from Foxhole Coppice, Monkhopton, and the other from Hudwick Dingle 1. About the former nothing further can usefully be said, but the latter (P.29725 ; Pl. 42, figs. 3, 3*a*) is a fragment of the dentigerous margin of the lower jaw of the type usually referred to " *Ischnacanthus kingi* " and is recorded under that genus by Dineley (1953 : 167).

The name " *Ischnacanthus kingi* " has long been familiar to workers on the Lower Old Red Sandstone of the Welsh Borders, and a practice has grown up of labelling thus all fragments of big acanthodian jaws, and occasionally the term has appeared in print in faunal lists (King, 1934 : 540 ; White, 1945 : 212) ; but no such species has been described, and it is now clear that more than one species is involved.

The first mention of it occurs in 1917 (King & Lewis, 1917 : 97) where it is stated in a footnote that it was " since described in Geol. Mag., dec. 6, vol. IV (1917), p. 74 ". This reference is to a brief note by A. S. Woodward on " *Plectrodus* ", on the second page of which he thanks " Mr. Wickham King for the opportunity of examining the microscopical structure of an unusually large specimen, probably of a new species, which he has recently found in the Downtonian of Baggeridge, S. Staffordshire ". No specific name is mentioned here and " *Ischnacanthus kingi* " remains a *nomen nudum*. However, there are many interesting specimens so labelled in Wickham King's collection and they and others subsequently collected are described below as belonging to two species.

Ischnacanthus kingi sp. nov.

(Pl. 42, fig. 4 ; Text-fig. 7)

Diagnosis. An *Ischnacanthus* of very large size with massive jaws greatly thickened along the upper and lower margins. Teeth acuminate and generally round in section ; the smaller teeth relatively large, about one-half or two-thirds the size of the larger teeth.

HOLOTYPE. Imperfect lower margin of palato-quadrate (P.12202) from Baggeridge (zone I.2 of Wickham King).

LOCALITIES AND MATERIAL. The holotype and a second specimen from Baggeridge (zone I.2 of Wickham King) are all that are definitely assigned to this species. The palato-quadrate margin of a small fish from the Ludlow Bone-bed at Brockton, Shropshire (P.33879) and a fragment of a small jaw-bone from Man Brook 2 (P.17395) are rather similar. None is known from the Clee area.

DESCRIPTION AND REMARKS. Clearly this species must be based on the specimen from Baggeridge (P.12202) to which King first applied the name and on which Woodward (1917) wrote his note. It is a very large bone that formed the lower border of the palato-quadrate and measures 10 cm. in length, although lacking a substantial part of both ends. It is 0·8 cm. in depth and shows the lingual side. Unfortunately the tooth-bearing surface is very imperfect and the dentition is represented by the remains of two large teeth, the broken bases of five others and a number of small teeth or their bases (Text-fig. 7).

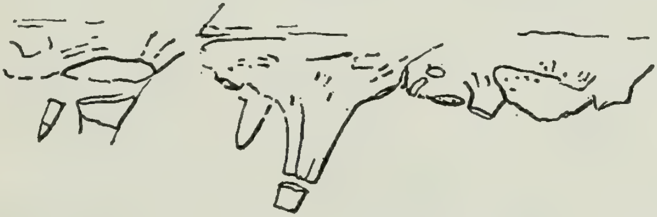


FIG. 7. *Ischnacanthus kingi* sp. nov. Part of dentition of upper jaw. Baggeridge Colliery, South Staffordshire. The holotype. P.12202. × 4·5.

The most complete tooth is about 0·5 cm. high, acuminate and nearly round in section. The sides show fine vertical ridges. The bases of some of the other large teeth are more oval and between them are the remains of much smaller sharply pointed round teeth, most of which line the vertical flange on the outer side, now broken away. None has a pulp-cavity but in cross-section they show a finely reticular pattern with numerous openings of canaliculi on the surface, exactly like the jaw-bone itself from which they arise gradually. They are apparently outgrowths of the bone-substance, like arthrodire teeth, and not true teeth ankylosed to the jaw.

The second specimen from Baggeridge Colliery is an almost complete right lower jaw of a much smaller fish (Pl. 42, fig. 4). It is just under 7 cm. long and 1·8 cm. at its deepest. Watson's (1937 : 79, pl. 9, figs. 3*a*, 3*b*) description of the same bone in the very much smaller *I. gracilis* applies very closely except that this bone shows the outer instead of the inner side of the jaw. The thickened lower margin is deep laterally and so is the upper dentigerous margin. The latter is twisted and almost vertical at the articular end, thus forming a groove for the passage of powerful jaw muscles which were accommodated in the hollow between the two ridges, but in this specimen the thin wall connecting them has been lost. Beyond the point where the two ridges meet there is a long anterior beak-like prolongation, triangular in section and hollow, the " anterior ossification " of Watson, which is externally continuous with the rest of the jaw. The tooth-bearing area is very short, but not quite as short as shown in the figure, since a part behind, as far as the vertical crack, has been broken away. The teeth are of two sizes, as before, and are part of the vertical outer flange. They are narrow and acuminate, but show signs of wear at the tips.

The species is not easily defined in distinction from *I. gracilis*, apart from its great size, since so little is known of it, but the difference between the large and smaller teeth seems to be less here than in the type-species, although the degree of wear may be misleading.

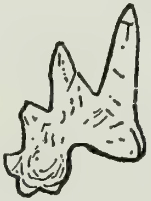


Fig. 8. *Ischnacanthus wickhami* sp. nov. Median spiral tooth-roll. Man Brook 7, Trimpley. P.17397. × 1·5.

Ischnacanthus wickhami sp. nov.

(Pl. 42, figs. 1–3 ; Text-fig. 8)

Diagnosis. An *Ischnacanthus* of great size, with the teeth laterally compressed and sometimes much elongated.

Holotype. Part of right palato-quadrate margin with teeth (P.24625) from Gardener's Bank, Cleobury Mortimer.

Localities and material. The only Clee locality is Hudwick Dingle 1. The great mass of the material is from Man Brook 6 and 7 near Trimpley (King's zone I.6). Only single specimens have been obtained from comparable strata elsewhere, the holotype from Gardener's Bank ; P.17409 from near Abberley, Worcestershire, and P.23817–18 from Hay Castle, Brecon. The species would appear to be rather later in range than *I. kingi*.

Description. All the specimens of jaws labelled " *Ischnacanthus kingi* " by Wickham King collected from other localities than Baggeridge Colliery (and presumably subsequently to his collection from that locality) show a very different type of dentition in which the teeth are laterally compressed and sometimes elongated into long shearing teeth. This is best seen in the holotype, a fragment from the right side, from Gardener's Bank, (not collected by King) which has been removed completely from the matrix by acetic acid (Pl. 42, figs. 2, 2*a*). The smaller teeth are very irregular and include the shearing teeth and, as in the preceding species, form part of the upturned lateral margin of the smooth horizontal palatoquadrate shelf which increases in width as it goes forward. As Watson (1937 : 80) states of *I. gracilis*, the series of smaller teeth is " interrupted by the large teeth which are rooted on the surface of the jaw and rise from it with their outer surfaces in complete continuity with the labial flange ". Most of the specimens of this species are jaw fragments of various sizes and were collected by King at Man Brook near Trimpley. They are very imperfect and many show a remarkable degree of wear, the teeth often being reduced to mere stumps (Pl. 42, fig. 1), so it is clear that they were not replaceable and the life of the fish depended on their durability.

Among the remains of the lower jaw is the only specimen from the Clee district, part of the oral margin of the left ramus from a relatively small fish (Pl. 42, figs. 3, 3*a*). All the smaller teeth on the labial flange are laterally compressed and variable in size ; while of the two larger teeth, one is much wider than the other. The oral shelf widens rapidly forwards and bears an irregular series of denticles internally to the main teeth. The bone shows on its outer side the marked oblique groove noted in *I. kingi* above.

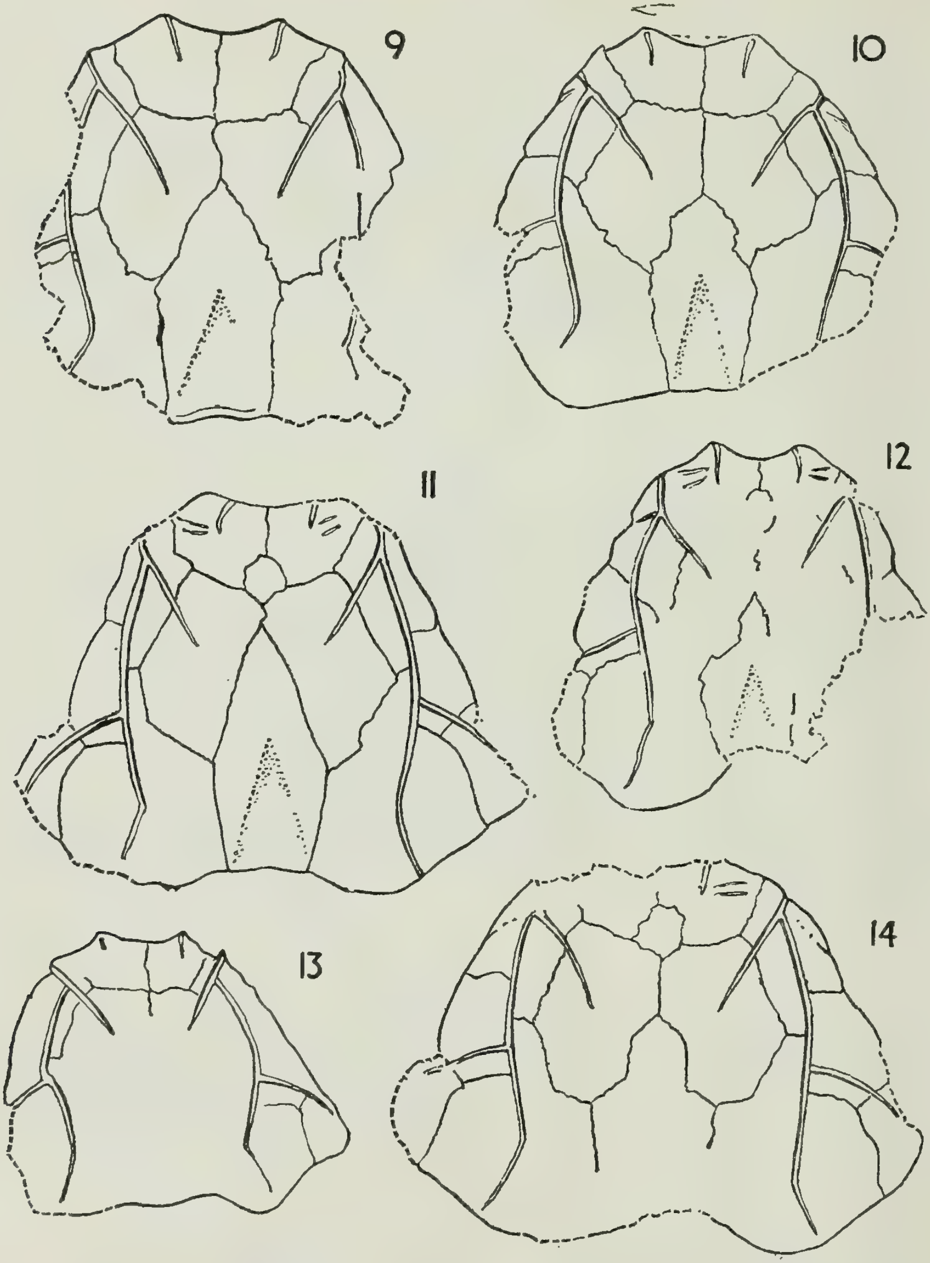
Associated with the jaw-bones at Man Brook is a large symphysial spiral (Text-fig. 8) closely resembling that on the lower jaw in Watson's (1937, text-fig. 11) restoration, and half a dozen smaller ones, as well as a large curved anterior dorsal spine (P.14444) about 9·5 cm. long and parts of another (P.16555). Smooth convex scales are commonly associated with the other parts of the fish.

REMARKS. As already noted these specimens are very like the comparable parts of *I. gracilis* described by Watson (1937). The teeth in their various forms closely resemble those on the minute jaws from the Upper Ludlow " Beyrichienkalk " figured by Gross (1957 : 13, pl. 5, figs. 2–9) as " *Nostolepis* ", a genus based on scales supposedly of coelolepid origin (Pander, 1856 : 68, pl. 6, fig. 7), but the associated symphysial spirals are very different. The rounded form of some of the teeth described by Gross (1947 : 148, pl. 9, fig. 3), so apparent in those from Man Brook, seems to be due to wear.

Order ARTHRODIRA

Rare specimens that have been referred to arthrodires have been identified from six or seven localities. They are all small fragments of plates or spines that cannot be assigned to a particular genus, although most are clearly arctolepid, with three exceptions which are all referable to *Kujdanowiaspis anglica.* The localities for the indeterminable remains are :

Batch Brook (800 ft. above " *Psammosteus* " Limestone).
Clee St. Margaret (675 ft. above " *Psammosteus* " Limestone).
? Cold Weston Quarry (850 ft. above " *Psammosteus* " Limestone).
Criddon Bridge (5 ft. above " *Psammosteus* " Limestone).
Poston Old Quarry (800 ft. above " *Psammosteus* " Limestone).



FIGS. 9–14. *Kujdanowiaspis anglica* (Traquair). Outlines of six skull-roofs to show range in variation of component plates. All nat. size. (9) P.27550, Silvington Waterfall. (10) No. 42147, Cradley, Herefordshire. (11) Geol. Surv. No. 4740, " Hereford " (probably Heightington). (12) No. 38032, Heightington, Worcestershire. (13) P.29417, Cradley (cast of holotype in Royal Scottish Museum, No. 1926. 57·2.) (14) Geol. Surv. No. 4417, Heightington, Worcestershire.

Genus ***KUJDANOWIASPIS*** Stensiö, 1942

Kujdanowiaspis anglica (Traquair)

(Pl. 45, fig. 7; Text-figs. 9–15)

Localities and material. Three specimens only may be certainly attributed to this species: the external impression of a head-shield from Silvington, Waterfall (600 ft. above "*Psammosteus*" Limestone); the internal impression of the left anterior quarter of the ventral armour from Hoptongate (700 ft. above "*Psammosteus*" Limestone) and an anterior ventro-lateral plate from Rea Brook, New House Farm (650 ft. above "*Psammosteus*" Limestone).

Description. The impression of the skull (P.27550; Text-fig. 9) is finely preserved and on it may be traced the outlines of the component bones and the course of the sensory canals. It may be compared with the sketches of the other known skull-roofs of this species (Text-figs. 10–14) which show the great variation in the shape of the individual plates (see also Text-figs. 42, 43).

The second specimen, from Hoptongate (P.27097; Text-fig. 15) shows, mostly as internal impressions, the left anterior ventro-lateral plate, the anterior median ventral plate and part of the inter-lateral plate with coracoid process of a young fish. The whole is only 2·8 cm. long, and the tubercles of the ornamentation are correspondingly fine. It is very much as in Stensiö's (1944 : 60, text-fig. 17B) restoration of a Podolian form.

The last, from Rea Brook, New House Farm, Neenton, is a very well preserved triangular piece consisting of part of the right anterior ventro-lateral plate with the spinal plate and a very small fragment of the inter-lateral plate (P.29821; Pl. 45, fig. 7). It measures 3·7 cm. across and 2·8 cm. from the anterior margin to the

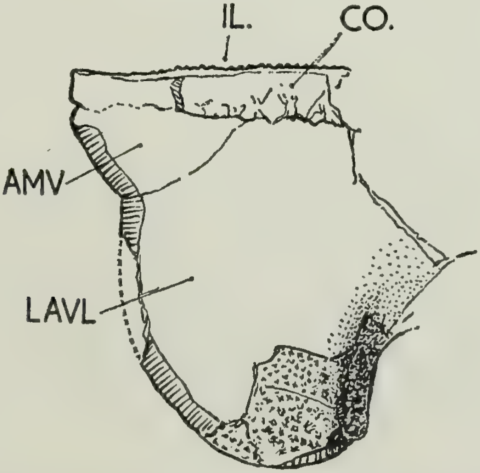


Fig. 15. *Kujdanowiaspis anglica* (Traquair). Left anterior quarter of the ventral armour of a small fish, largely an internal cast. AMV, anterior median ventral plate. Co, coracoid. IL, interlateral plate. LAVL, left anterior ventro-lateral plate. Hoptongate. P.27097. × 2.

pectoral sinus. Apart from the pectoral sinus and the contact with the spinal plate, the margins are missing, but the spinal plate is complete except for the free portion. In no important feature does it differ from specimens from elsewhere, but the ornamentation, developed by acid, is very clear. On the AVL plate the rounded tubercles tend to run in lines very roughly parallel with the margins. Most are somewhat rubbed but it can be seen that they were rather small and low with crinkled bases. The tubercles along the free lateral margin of the spinal plate are larger and taller, and their size and arrangement in numerous parallel longitudinal rows mark them off from the ornamentation on the undersurface.

REMARKS. All these specimens may be considered typical of this as yet indifferently described species, which is widely spread, although generally rare, in corresponding strata in Herefordshire.

Arthrodires range throughout the whole of the lower group of the Ditton Series, extending into the middle of the upper group, i.e. from 5 ft. to 1,100 ft. above the "*Psammosteus*" Limestone; and *K. anglica* is known from 600 ft. to 1,100 ft. above the "*Psammosteus*" Limestone.

II. FAUNA OF THE UPPER GROUP OF THE DITTON SERIES

The most striking feature of the fauna of these upper beds is the high incidence of new forms, ten out of twelve named species, four of them here referred to new genera. On the other hand *Kujdanowiaspis anglica* is a rather unexpected survival from the lower beds, where it is widely distributed along the Welsh Marches, although rather rare; and *Pteraspis* (*Cymripteraspis*) *leachi* provides a useful means of correlation with continental strata of Lower Siegenian age (Schmidt, 1960 : 140).

Class AGNATHA

Order HETEROSTRACI

Genus ***PROTASPIS*** Bryant, 1933

Subgenus ***EUROPROTASPIS*** nov.

Denison (1953 : 318) has re-defined the genus *Protaspis* in the light of new information, but his diagnosis is based largely on the American species. He notes, however, that in *P. arnelli*, the only well-known form from Europe, that the position of the branchial opening and the form of the cornual plate are different, but nevertheless states that these differences "are hardly adequate to characterize a new genus" in spite of the possibility that the Podolian species "may have acquired its *Protaspis*-like characteristics independently" (1953 : 326). These features seem to be worth at least subgeneric distinction, especially as there are other differences in *P. crenulata*, particularly in the pre-oral field and in the squamation. I therefore propose a new subgenus, *Europrotaspis*, to include the new species from Shropshire and *P. arnelli* from Podolia.

The difference between the pre-oral fields is indeed most marked, for in the English species it is large and flat (Text-fig. 17), whereas in the specimen referred to *P. bucheri* (Denison, 1953, text-fig. 78) it is virtually non-existent.

There are two most puzzling features about the scales of *P. crenulata* (all isolated ; there are no scales recorded of *P. arnelli*) which seem to separate it widely from the American species. The more marked is the very large size of the associated ridge-scales, which, relative to the largest plates known, are much greater than those figured in the tailed specimens of the American species, although these are large compared with those recorded in other pteraspids (Bryant, 1934, pls. 22, 23, 24, fig. 1 ; Denison, 1953, text-fig. 74). Even more surprising is the fact that a number

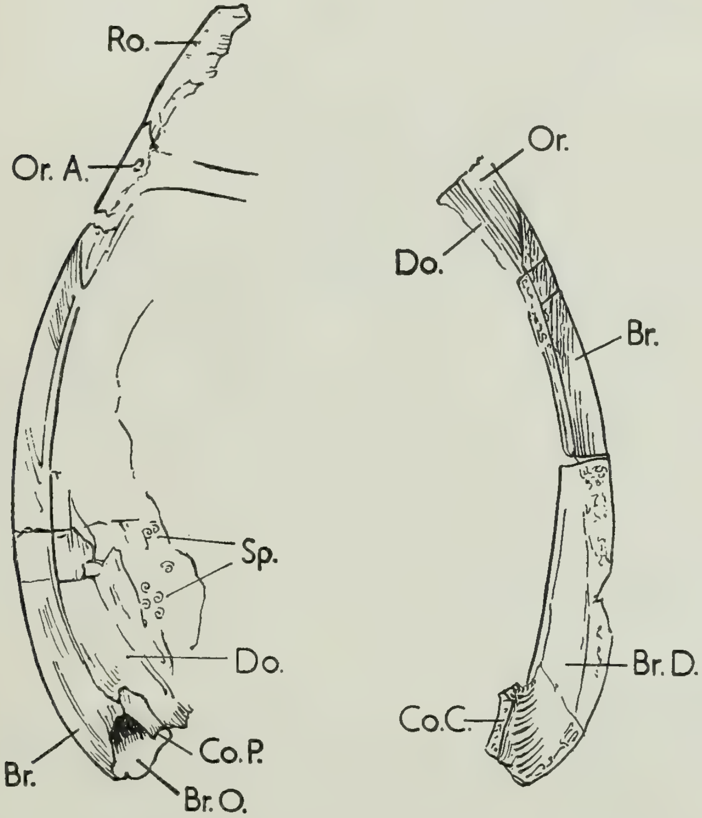


FIG. 16. *Protaspis* (*Europrotaspis*) *crenulata* sp. nov. Imperfect dorsal shield. The holotype. Besom Farm Quarry. P.28801. Slightly enlarged. *Br.*, branchial plate ; *Br.D*, branchial duct ; *Br.O*, branchial opening ; *Co.C*, cornual contact surface on branchial plate ; *Co.P*, cornual plate ; *Do*, dorsal disk ; *Or*, orbital plate ; *Or.A*, orbital aperture ; *Ro*, rostrum ; *Sp*, shells of *Spirorbis* attached to undersurface of dorsal disk.

of them are strongly asymmetrical, with a marked keel and almost flat underside, which clearly suggest a lateral series—an entirely novel feature in pteraspids unless Zych's (1931, figs. 41, 49) restorations of Podolian species of *Pteraspis* are to be taken seriously. The existence of a lateral series of ridge-scales is supported by the shape of the branchial plates which corresponds to that of the scales, for there is an acute longitudinal keel separating the flat undersurface from the convex upper surface.

Whether these characters occur in all the European forms is not yet known, but the shape of the branchial plates in the Podolian *P. arnelli* as restored by Brotzen (1936, text-fig. 3) suggests that they do occur in that species at least.

There are two other points in Denison's (1953) diagnosis that may be called into question : the first is the length of the rostrum, which is stated to be " very short to moderately long ". Presumably the " moderately long " refers to *P. priscillae*, but the reference of this species to *Protaspis* seems very doubtful, for none of the critical hinder part of the shield is known. More important is the supposed shape of the tail, which Denison describes as being short and " nearly symmetrical ". The irregularity of the tail that he figures (Denison, 1953, text-fig. 74), not only in shape but also in the arrangement of the marginal scales, proclaims it to have been malformed (compare that of " *Malania* ", the second specimen of the living coelacanth—see White, 1953 : 114, text-fig. 3). The diminution in size of the scales on the tail of *Pteraspis* is perfectly regular, like the shape itself, and there are small fulcral scales on both margins of the lobe. Either the tail of this specimen was injured when young and has grown irregularly, or it has been bitten off and partly regenerated. Moreover, there is reason to believe that the specimen is figured upside down, for the scaling at the end of the rows, as illustrated, runs upwards and backwards instead of the normal downwards and backwards, and in *Pteraspis* it is the dorsal series of ridge-scales that tend to be long and narrow and the ventral series that are short and deep (the depth of the " upper " series as figured by Denison is clearly seen in his figure 74A, although not in his restoration). When a laterally compressed tail is twisted at right angles to a rigid body, it is not always easy to see which way it has gone.

DIAGNOSIS. *Europrotaspis* is defined as a subgenus of *Protaspis* in which the cornual plate is reduced to a short narrow element lying between the dorsal disk and the end of the elongated branchial plate ; the branchial opening is large, terminal in position and partly directed upwards ; the snout short with a well-developed wide pre-oral field having a slight posterior median ridge ; ridge-scales probably extremely large relative to the body-size and arranged, in addition to the usual symmetrical dorsal and ventral series, in very asymmetrical lateral series following the branchial plates, which have an acute longitudinal keel and a flat undersurface.

SPECIES. *P. crenulata* sp. nov., the subgenotype ; *P. arnelli* Brotzen and possibly *P. wiheriensis* Brotzen and *P. rotunda* Gross.

Protaspis (Europrotaspis) crenulata sp. nov.

(Pls. 43, 44 ; Text-figs. 16–33)

DIAGNOSIS. An *Europrotaspis* with rostrum rounded and median length of upper surface contained about four and a half times in that of dorsal shield; dorsal disk with maximum breadth somewhat less than median length and narrowing only moderately towards anterior end. Dentine ridges of superficial "ornamentation" coarse, average 5–6 per mm., when unworn A-shaped with relatively coarse lateral denticulations continued on to the ridges, giving a crenulate appearance.

HOLOTYPE. An imperfect dorsal shield (P.28801).

MATERIAL. In addition to the holotype, about 70 specimens, including a dorsal disk; one almost complete and two fragmentary ventral disks; three incomplete branchial plates; 34 isolated scales and about 30 other fragments.

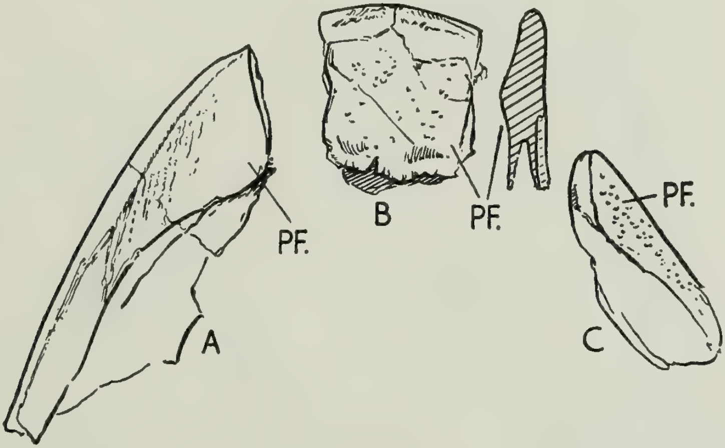


FIG. 17. *Protaspis* (*Europrotaspis*) *crenulata* sp. nov. A, B, C, three fragments of different rostra, ventral view, with median longitudinal section of centre fragment, showing the pre-oral field (*PF*). Besom Farm Quarry. P.33832, P.28802, P.28825 respectively. × 2·25.

LOCALITIES. The most important is the old quarry ¼ mile SE. of Besom Farm, Wheathill, Shropshire; another is Upper Overton Quarry, nearly 5 miles to the north-east. Exposures at Prescott Reaside and Farlow Brook Bridge have also yielded some good specimens. Scales and fragments have been found at three or four other places in the neighbourhood.

DESCRIPTION. The holotype is an eroded and primarily imperfect dorsal shield (Text-fig. 16). The right side of the rostrum and most of the right orbital plate were lost before fossilization, and subsequently almost the whole of the dorsal disk and the dorsal side of the right branchial have been removed by weathering, the specimen being on a loose surface block. The left branchial plate with the minute cornual is very well preserved, the posterior half being uncrushed (as was presumably the whole specimen) and preserved in the round.

An interesting feature of this specimen is the occurrence of a number of small spiral shells attached to the inner surface of the dorsal disk (Pl. 43, fig. 3; Text-fig. 16, *Sp*). These are apparently the remains of *Spirorbis* sp. and indicate that the carapace had lain exposed on the bottom for some considerable time after the decay of the soft parts and before being covered over. This perhaps accounts for the fractured state of the rostrum.

The length of the fossil from the broken tip of the rostrum to the end of the left branchial plate is 9·2 cm. and the maximum breadth, at about 3·5 cm. in front of the hinder end of the branchial, is 7 cm.

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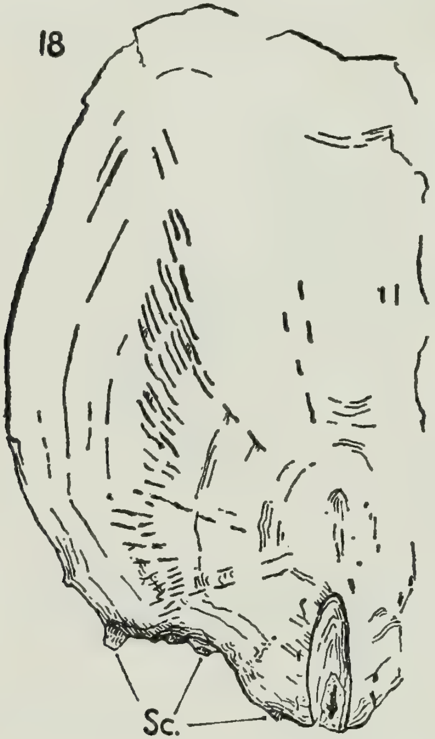

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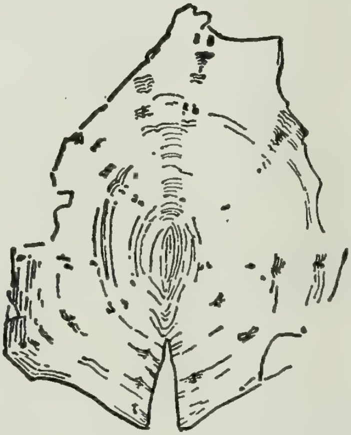


Protaspis (*Europrotaspis*) *crenulata* sp. nov.

FIG. 18. Imperfect, flattened dorsal disk of adult, possibly aged animal, showing base of dorsal spine and small scales (*Sc.*) attached to left hinder margin. Upper Overton Quarry. P.29415. × 1·5.

FIG. 19. Imperfect part-grown dorsal disk in impression with indications of sensory canals. Besom Farm Quarry. P.26313. × 1·5.

Probably little has been lost of the rostrum in length, for fragmentary specimens of this plate indicate that it was very much rounded in front (Text-fig. 17). If so, its length was contained about four and a half times in the total length of the shield, omitting the dorsal spine.

The orbital plates were small with very small orbits, but the mesial processes were broad and certainly met the pineal plate, which is unknown, completely separating the rostrum from the dorsal disk.

The anterior margin of the disk is shallowly but widely indented with rounded corners, and the posterior margins are sigmoidally excavated (Pl. 43, fig. 1; Text-fig. 18). In this fully grown specimen a number of very small scales are fused to the hinder margin, the largest being immediately behind the cornual plate and fitting on to a short emargination of the disk. These small scales are probably no more than a manifestation of old age, which is often shown in compression, fusion and other irregularities commonly seen along the margins of the disks of pteraspids. They have nothing to do with the definite structures which Denison calls " posterior scale-like process of cornual plate ".

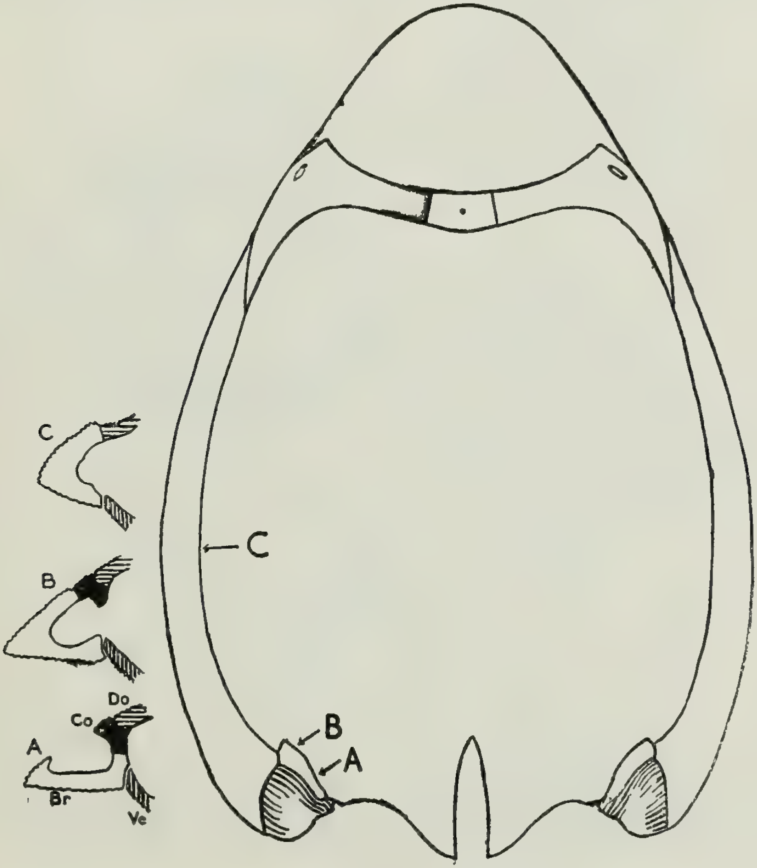


Fig. 20. *Protaspis* (*Europrotaspis*) *crenulata* sp. nov. Restoration of dorsal shield in outline, with enlarged cross-sections through branchial plate, etc., at A, B, and C. × 1 approx. *Br*, branchial plate; *Co*, cornual plate; *Do*, dorsal disk; *Ve*, ventral disk.

The sides of the dorsal disk are moderately convex, particularly in the hinder quarter as the cornual plate is approached, for which there is an emargination varying in definition with age, being most marked in the oldest specimens (Text-fig. 16), scarcely perceptible in the half-grown (Text-fig. 19), and altogether absent in the young which have the usual rounded outlines (P.28881).

The socket for the dorsal spine is relatively short in the adult, occupying about one-fifth of the median length of the dorsal disk. Of the spine itself only the basal portion is known (Pl. 43, fig. 1 ; Text-fig. 18 ; P.29076), but to judge from these fragments it was clearly stout and low, coming off the disk at about 30°, and probably short.

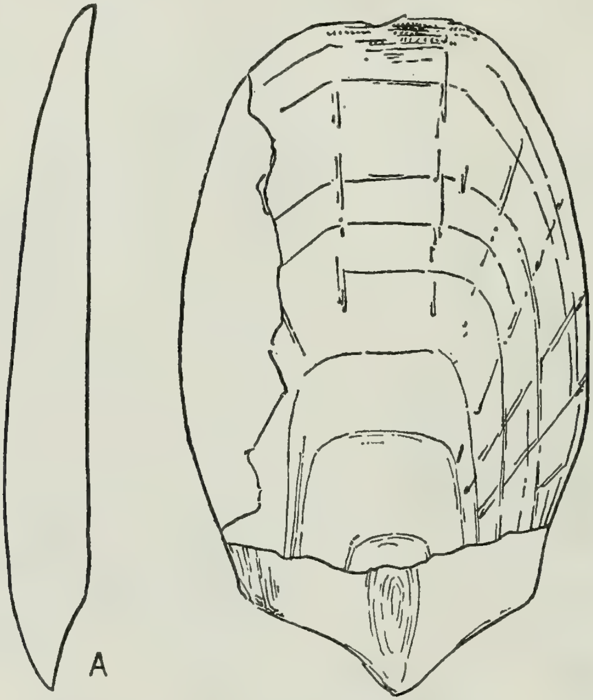
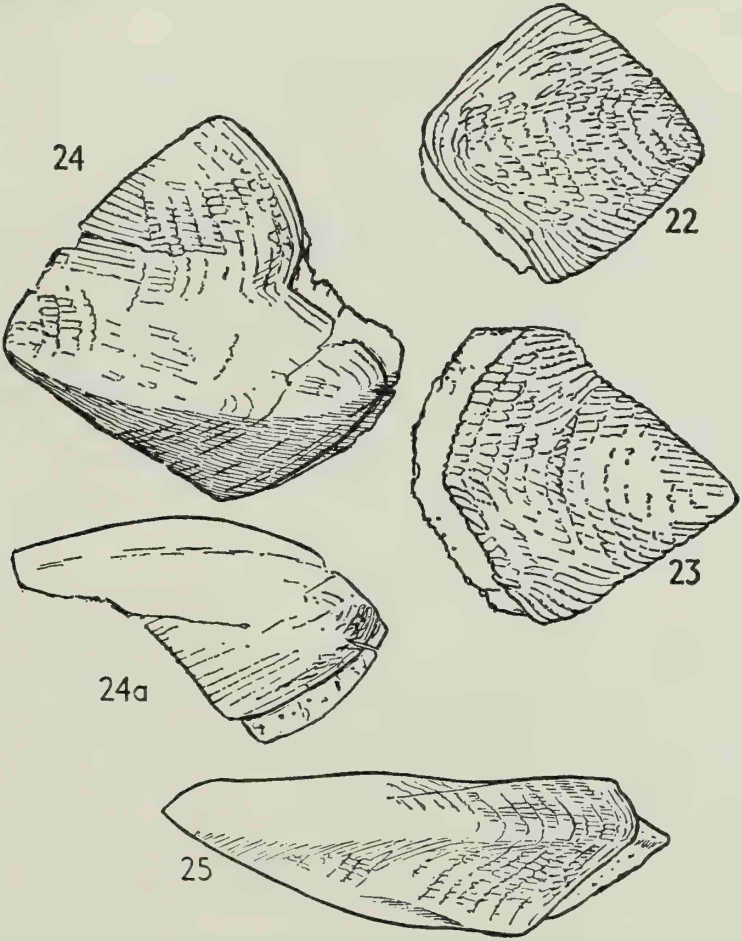


Fig. 21. *Protaspis* (*Europrotaspis*) *crenulata* sp. nov. Ventral disk, mostly in impression, with posterior marginal area added from second specimen. A, side view in outline. Besom Farm Quarry. P.26311, P.28803. Slightly enlarged.

The degree of convexity of the dorsal disk is not known, for this plate is largely abraded in the holotype and the other specimens are flattened.

The branchials are massive plates with a convex upper surface separated by an acute lateral longitudinal keel from the undersurface which to the rear becomes flattened and almost horizontal (Pl. 43, fig. 2 ; Text-figs. 20A–C). The upper margin is, as usual, firmly attached to the dorsal disk over most of its length, to the orbital plate in front, and to the cornual plate behind, but contact with the last-named is only a millimetre or two long. The contact of the lower flange, which is wider than the upper, met the ventral disk along a slightly concave free edge.

Except at the posterior end where dorsal and ventral inner margins were very briefly connected by the diminutive cornual, the branchial plate was open to the body and formed the common branchial duct, deep behind and shallowing forwards. The upper surface shows remains of two of the ridges dividing branchial pouches.



Protaspis (*Europrotaspis*) *crenulata* sp. nov.

Figs. 22, 23. Flank scales. P.29068, P.27516. × 7·5.

Fig. 24. Supposed anterior ventro-lateral ridge-scale in side view and (*a*) from below. P.27515. × 7·5.

Fig. 25. Supposed ventro-lateral ridge-scale. P.28884. × 2·8.

All from Besom Farm Quarry.

The external branchial aperture opens obliquely upwards, being floored by the longer, lower flange of the branchial plate and walled medially by the cornual, precisely as in the Podolian species, *P. arnelli* Brotzen (1936, text-fig. 3).

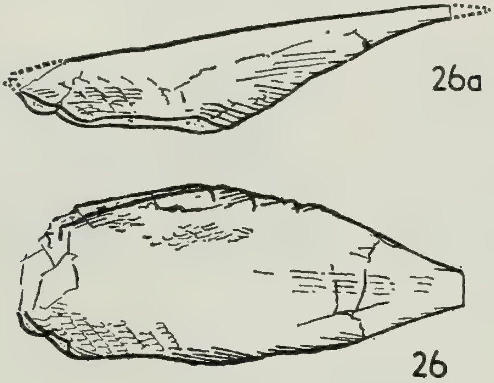
The ventral disk (Text-fig. 21) is of the type usual in most pteraspids, ovate in outline with the posterior end bevelled on each side to form a blunt median projection. The plate is moderately convex along both axes, with the anterior end flatter than the hinder, like the dorsal disk. As in all these animals the edges were free, smooth and slightly convex, and the plate was attached to the branchials only by soft tissues, which explains why the ventral disk is always found isolated except in rare instances when the whole creature is preserved. The reason for this looseness of attachment was probably to provide flexibility to allow rhythmic movement as an aid to breathing, comparable to that provided by the very different branchial mosaic in cephalaspids.

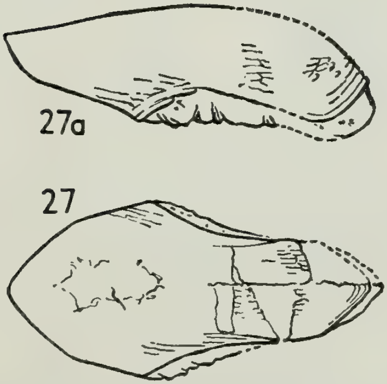
The only other skeletal parts preserved are isolated scales. The flank-scales (Pl. 43, fig. 5; Text-figs. 22, 23), of which there are about 25 examples, are of the usual type in pteraspids, thick, more or less diamond-shaped with a narrow overlapped margin lacking the external layer along one or both of the anterior margins of the quadrate ornamented surface (cf. White, 1935, pl. 27, text-figs. 61, 62; 1938, text-figs. 6–9; 1950*b*, text-figs. 10–13). They vary somewhat with their position on the body (e.g. P.26316, P.27517, P.28826–27, P.28864–65, P.28905, P.29086). Compared with the associated plates of the carapace, of which none is substantially larger than those of the holotype, these scales are very large indeed: relatively they are twice as large as those in the complete specimens of *Pteraspis* (*P.*) *rostrata toombsi*, and in actual size they come within the range of those of the very much larger *P.* (*Cymripteraspis*) *leachi*, which occurs with them. Fortunately the pattern of the ornamentation in the two species is distinctive.

The curious double flank-scales noted in species of *Pteraspis* (White, 1935: 413; 1950, text-figs. 13, 14) are also present in *Protaspis* (*Europrotaspis*) *crenulata*, but here some at least seem to have formed part of a definite series. These very large scales, of which the one shown in Text-fig. 24 is 1·1 cm. high over the curve, have a lower flange bent almost at right angles to the lateral face, and it seems evident that they formed the anterior part of a ventro-lateral series of ridge-scales covering the angle between the sides and the more or less flat undersurface, following behind the even more angular branchial plates (Text-fig. 20A–C). This row of asymmetrical scales formed a graded series (Text-fig. 24; Pl. 44, fig. 3; P.28874) to scales of very elongated form but still notably lacking in symmetry (Text-fig. 25).

The median ridge-scales (Text-figs. 26, 27; P.26315, P.28885) attain the same astonishing size, up to 2·5 cm. in length, and apart from their obvious symmetry, they are distinguished by the fact that the overlapped margin continues along the whole of the sides of the attached surface, which in the most elongated specimens is much less than half the total length, for the hinder part is raised into a free spine with the underside flat and ornamented like the upper surface. By analogy with *Pteraspis* (White, 1935: 417–418) the elongated scales with the free ends may be assigned to the dorsal series, the broader to the ventral. All the specimens show signs of wear along the central area. A juvenile dorsal scale, only 1 cm. long (Pl. 44, fig. 2), has an attached surface of only 0·4 cm. and this is deeply hollowed out with a median foramen. There were no overlapped margins.

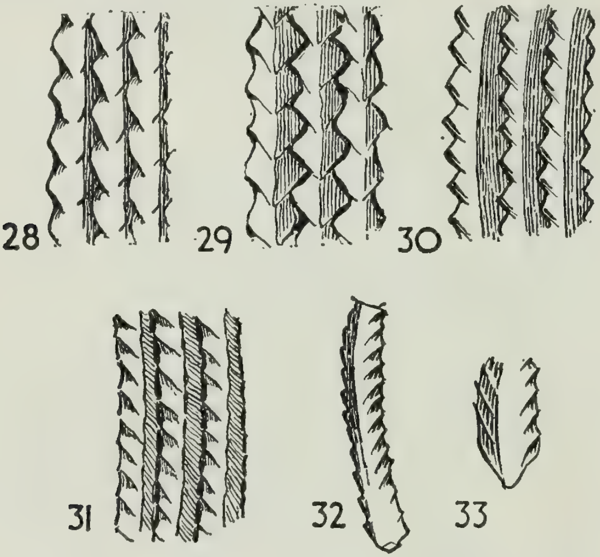
There is no doubt that these scales belong to this species, the ornamentation makes that clear, but as in the similar case of *Pteraspis leathensis* White (1950 : 79), there must be some uncertainty as to the relative sizes of the scales and plates owing to the possibility of water-sorting. As in the *Pteraspis*, however, the relative maximum sizes of plates and scales do not vary substantially from one locality to another.





FIGS. 26, 27. *Protaspis* (*Europrotaspis*) *crenulata* sp. nov. Dorsal and ventral ridge-scales respectively, in direct and (*a*) restored side-view. Besom Farm Quarry. P.28828, P.28886. × 3.

The ornamentation on the plates of the carapace and on the scales is of the usual ridge-and-furrow type found in all the pteraspids, but is coarser than in most species, the ridges in general running as few as 5–6 per mm. (except, as usual, near the centre of plates where they are often fewer, and near margins, particularly the postero-lateral areas of the disks, where they are more numerous). The ornamentation follows the normal pattern on all the plates but some of the disks show extreme irregularity in the centre. In the ventral disk figured in Pl. 43, fig. 4 the greater part of the plate, instead of being covered by the usual series of ridges running parallel with the front and sides, is divided into two by a longitudinal series, which meets the normally disposed series at the margin almost at a right angle. It was an arrangement such as this constantly occurring in *Pteraspis dixoni* that led Stensiö (1958 : 292) in the belief that such a pattern signified a different mode of development, to place this otherwise obvious species of *Pteraspis*, not only in a new genus, *Penygaspis*, but in a different Order, the Traquairaspida. As an irregularity it occurs occasionally in other species of pteraspids.



Protaspis (*Europrotaspis*) *crenulata* sp. nov.

FIGS. 28–33. Variations in the ornamentation. All × 40 approx. (28) From front end of dorsal disk. Besom Farm Quarry. P.28808. (29) From posterior end of ventral disk. Besom Farm Quarry. P.28809. (30) From undetermined fragment. Farlow Brook Bridge. P.29003. (31) From top end of branchial plate, medial side. Besom Farm Quarry. P.29076. (37), (38) From anterior and ventro-lateral areas of a scale. Besom Farm Quarry. P.29077.

The disks of the larger, and presumably old, specimens of *Pr.* (*E.*) *crenulata* show another deviation from the normal pattern near the anterior margin, where, instead of ridges, there are parallel bands of short segments at right angles (Pl. 44, fig. 7).

As is often the case, the pattern on the scales shows some specific individuality (Text-figs. 22–27). On the flank-scales the ridges run lengthwise across as usual and are divided over most of the exposed surface into short lengths by arched grooves parallel with the anterior margin at intervals that increase slightly to the rear. What is unusual is that the grooves do not reach the lower angle nor sometimes the top. The segments of ridges between each pair of grooves do not lie in line with those next to them but roughly alternate with them.

In some scales a few ridges run in front parallel with the margin, while in others this area is covered irregularly with short, broad segments.

A similar type of ornamentation is borne by the ridge-scales, but the increase in the spacing of the grooves towards the posterior point is more marked.

One feature clearly distinguishing this ornamentation is that the ridges themselves are ornamented, for in all British species of *Pteraspis* in which the ornament has been described in detail the very fine lateral denticulations which characterize the ridges in this genus lie in the grooves between them, and the ridges themselves, whatever their shape in cross-section, are absolutely smooth.

In *Pr.* (*E.*) *crenulata* the denticulations are continued on to each side of the ridges, which when fresh are sharply A-shaped (Pl. 44, fig. 4 ; Text-figs. 28–33). When slightly worn the ridges have a beaded appearance, allowing small fragments to be identified with ease (Pl. 44, fig. 5). Further wear, which is usual over much of the larger plates, may obliterate this feature and the ridges become flat and plain resembling those of other pteraspids in this condition.

It is probable that this ornamentation, or a variant of it, is to be found in other, if not all species of the subgenus, and possibly of the genus. A specimen referred to *Pr.* (*E.*) *arnelli*, kindly lent to me by Professor Stensiö, clearly shows a beaded ornament (Pl. 44, fig. 6).

The sensory canal system so far as it is known is exactly as in *Pteraspis* (Text-figs. 18, 19, 21). In the adult the pores opening onto the external surface are often very obscure except those of the outer longitudinal lines, where they are, on the contrary, extremely long and conspicuous. The median anterior loop on the ventral disk reaches far backwards and the medial branches of the marginal lines are also long.

Remarks. The first fragments of this new pteraspid were found by Professor L. J. Wills some years ago. It was then regarded as an unusual form of *Pteraspis* itself, useful as providing an easily identified marker of post-*crouchi* Dittonian strata (see White, 1950 : 53, text-fig. 1) ; but the unique but imperfect dorsal shield found by Dr. Ball (described above as the holotype) shows that it has the long branchial plates and reduced cornuals typical of the genus *Protaspis*, first described from Wyoming (Bryant, 1933 : 294) and subsequently recorded from West Podolia, Belgium and possibly also from the Rhineland (Brotzen, 1936 : 20). More recently Denison (1953 : 318–350, text-figs. 71–83) has given an excellent account of the Wyoming species and added a number of new forms from Utah.

This species is easily separated by its general form from the other European species that have been referred to this genus. It is far less exaggerated in its shape than the continental species, which are very broad in the disks, while the rostrum is more rounded than in *Pr.* (*E.*) *arnelli*. An examination of the type-material of this latter species suggests that it does not present the curious form shown in Brotzen's (1936, text-fig. 6) restoration, but is more like that in the English species, nor is the socket of the dorsal spine, although short, enclosed by the dorsal disk.

Genus **PTERASPIS** Kner, 1847

Subgenus **CYMRIPTERASPIS** White, 1960

In recent years considerable attention has been paid to the oral region of the species of *Pteraspis*, and it is clear that the form of the pre-oral field is of much systematic importance. Hitherto *P. dunensis* and *P. leachi* have been associated in the same subgenus *Rhinopteraspis*, but the discovery of the large triangular pre-oral field in *P. dunensis* (Tarlo, 1958 : 8), comparable with that in *P.* (*Belgicaspis*) *crouchi* (White, 1956 : 8, text-fig. 1) separates that species widely from *P. leachi*, in which the pre-oral field is very small (White, 1956 : 8, text-figs. 1–4). As in *P.* (*B.*) *crouchi*, the pre-oral field in *P.* (*R.*) *dunensis* is a separate plate developed independently of the rostrum and very rarely preserved, whereas in *P. leachi*, as shown by recent re-examination of the original specimens, although a separate plate with its own concentric ornamentation, it is firmly attached to the rostrum in all the specimens known.

A further difference between *P. dunensis* and *P. leachi* lies in the cornual plate : in the former it has never been seen and must have been very small if it existed at all ; whereas in *P. leachi* it is long and fairly deep, but with scarcely any horizontal flange. *P. leachi* has also more horizontally protuberant orbital plates with a wide groove sharply demarcated running along the lower margin.

From the species referred to *Althaspis* Zych (= *Pseudopteraspis* Stensiö), *P. leachi* differs quite clearly by the possession of a small discrete pre-oral plate, which is concentrically ornamented but, apart from an external groove marking its outline, is, at least in adult specimens (the only specimens known), fused with the pre-oral margin (cf. White 1956, text-fig. 4 ; Stensiö 1958, text-figs. 136, 144, 157, 191*A* ; White 1960, pl. 2, fig. 1).

P. leachi has therefore been placed in a separate subgenus, *Cymripteraspis* (White, 1960 : 8).

Pteraspis (Cymripteraspis) leachi White

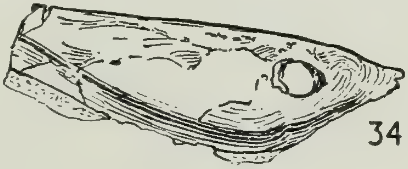
(Pl. 45, figs. 1, 2 ; Text-figs. 34, 35)

1938 *Pteraspis* (*Rhinopteraspis*) *dunensis* var. *leachi* White, p. 87, text-figs. 1–10.
1956 *Pteraspis* (*Rhinopteraspis*) *leachi* White, p. 6, text-fig. 3.
1959 *Pteraspis* (*Rhinopteraspis*) *leachi* White : W. Schmidt, p. 54, pl. 1, figs. 4–7 ; pl. 2, figs. 1–7 ; pls. 3, 4 ; text-figs. 4 (2), 10–13.
1960 *Pteraspis* (*Cymripteraspis*) *leachi* White, p. 8.

Localities and material. Fragments of this species are more widely spread in the Clee district than are remains of *Protaspis crenulata*, for they occur at the same eight localities and half a dozen more ; but the great majority are very trivial, and except at Prescott Reaside and Besom Farm Quarry, which account for more than half of the total of about 60, they are rare.

Description. The largest fragment, measuring only 4 × 3·5 cm., is from the right anterior quadrant of a dorsal disk from Lower Ingardine Ford (P.27548–49). The best specimens from Besom Farm Quarry are three pieces of branchial plate, each with part of the dorsal disk attached. The largest (P.28811) is about 3·7 cm. long and from the left side. It shows well the laterally flattened form of this plate characteristic of the species. The other two fragments are both from the anterior end of right branchials (P.33836–37). All show close resemblance to the corresponding parts in the original specimens from Swanlake Bay.

The only other specimens worthy of individual note are an imperfect right orbital plate (P.29198) and a good flank-scale (P.29261), both from Prescott Reaside. The orbital plate (Text-fig. 34) lacks the medial process, the anterior projection and the most posterior third of its length, measuring as preserved 2·0 cm. Nevertheless, it resembles closely the orbitals in the original specimens from Swanlake Bay (Text-fig. 35), being laterally protuberant and overhanging with a wide, sharply defined, suborbital groove running parallel with the inferior margin, above the very defective overlapped border. It clearly differs from the plate in *P.* (*Rhinopteraspis*) *dunensis* in which the groove is absent (Text-fig. 36).



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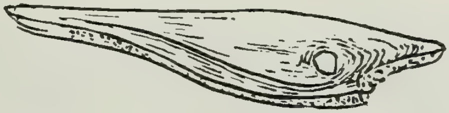

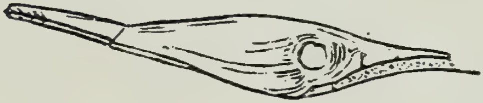

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Pteraspis (*Cymripteraspis*) *leachi* White

Fig. 34. Imperfect right orbital plate. Prescott Reaside. P.29198. × 3 approx.

Fig. 35. Restoration of right orbital. Based on P.18048. Swanlake Bay. × 2 approx.

Pteraspis (*Rhinopteraspis*) *dunensis* (Roemer)

Fig. 36. Right orbital. Emsian: Schleiden, Eifel. P.31629. × 2 approx.

The typically diamond-shaped flank-scale is small, measuring 0·6 cm. long and 0·7 cm. high without the anterior overlapped margin, which is imperfect (Pl. 45, fig. 2).

All the plates have the typical ornamentation of very fine, flat ridges so closely appressed that the minute lateral denticulations are rarely to be seen except on the scales. On the whole the ridges are slightly finer than on the Swanlake type-specimens, numbering 8–10 per mm. (except on marginal or central areas, where they are in all species finer and coarser respectively) as against 6½–9. As in the Swanlake scales the chevron-shaped grooves run parallel with the anterior margin and divide up the ridges on the exposed surface. These are evenly spaced at about 2·5 mm. intervals. Near the front border the ornamentation tends to be irregular.

Remarks. That these specimens are referable to *P.* (*C.*) *leachi* is evident. The slightly finer ornamentation may be a local variation, or it may have time significance. Specimens of this species discovered by Professor Ubaghs near Pepinster in Belgium (White, 1960 : 8) show the opposite tendency and are somewhat coarser in the ornamentation than the Swanlake specimens, which may, therefore, be intermediate in age. But even if there is such significance in this variation, it is not clear which way the series runs, for there is no field evidence in these widely separated localities that I know of, nor are there associated faunas at Swanlake or at the locality near Pepinster to indicate differences in age. However, on the analogy of the greatly increased coarseness in the ornamentation of the later species, *P.* (*Rhinopteraspis*) *dunensis*, it is perhaps more likely that the tendency is from fine to coarse, and that the Clee beds are somewhat older than those at Swanlake and those near Pepinster the youngest.

Order OSTEOSTRACI

Genus ***BENNEVIASPIS*** Stensiö, 1927

Benneviaspis salopiensis sp. nov.

(Text-fig. 37)

Diagnosis. A *Benneviaspis* of moderate size with maximum breadth of cephalic shield, without cornua, about one and a half times median length. Rostral margin rounded, lateral margins convex. Cornua unknown, but with narrow bases and almost certainly small. Pectoral sinuses of moderate width and depth. Interzonal part short with short and wide median projection, and negligible postero-lateral angles. Dorsal sensory field very large, almost reaching margin of posterior projection, somewhat wider than long, broadly lonzenge-shaped with well-defined lateral angles and slightly convex antero-lateral margins. Lateral sensory fields narrow with small postero-median angle.

Holotype. Imperfect cephalic shield in counterpart (P.29720–21). The only specimen.

Locality. Besom Farm Quarry.

Description. This specimen is in many respects badly preserved, but sufficient is present to show its unique character. The exoskeleton, as usual very thin, is in poor condition, the cornua are missing, the right margin defective and the whole somewhat distorted. As preserved, the shield is 5·5 cm. in breadth and 4·0 cm. in median length. The left eye is distorted but the right measures 4 × 3 mm.: they lie a little behind the mid-point of the shield, not far in front of the level of the pectoral sinuses. The sinuses are moderately deep and not very wide owing to the relative breadth and shortness of the interzonal part. The missing cornua have narrow bases and were probably short.

The hinder margin of the shield has a very wide median projection on each side of which the border is shallowly concave and meets the lateral margins in a right angle, so that the postero-lateral projections or angles are virtually absent.

Perhaps the most striking feature of the shield is the very large dorsal sensory field. It reaches from the pineal plate almost to the hinder border and is fan-shaped so that the posterior angle almost fills the median projection of the shield. The antero-lateral margins are slightly convex and the blunted lateral angles are roughly right angles. The length is 1·5 cm. and the breadth a little more.

The naso-hypophysial area is very well preserved and shows an interesting feature in that it is very short instead of the usual inverted key-hole pattern. The opening, which has a smooth raised rim, is 1·7 mm. long and on average 0·5 mm. wide, and clearly it would seem to represent only the anterior, hypophysial component. A short, well-defined suture runs for 1·5 mm. from the opening, backwards, with the fine but strongly marked ornamentation of intertwined elongated tubercles covering the area and arranged on either side of it : thus far there is no indication of a separate nasal opening and it is likely that none existed, the opening serving for both. This opening is in fact further back than usual, on the front slope of the nasal prominence instead of in the depression in front. The internal casts of this area may be seen in the type-specimens of *B. lankesteri* and *B. anglica* (see Stensiö, 1932, pl. 48), and indicate the same arrangement. The supposed existence of the independent nasal opening in this genus is probably due to the shearing off of the top of the eminence.

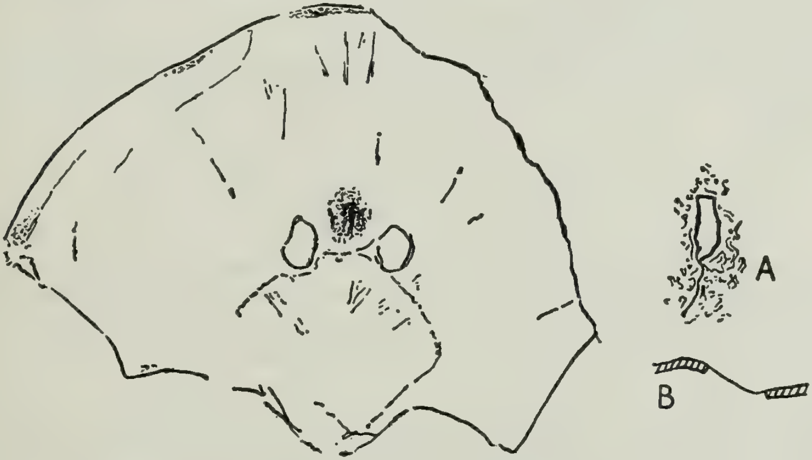


FIG. 37. *Benneviaspis salopiensis* sp. nov. Imperfect cephalic shield. A, Naso-hypophysial area, much enlarged. B, Longitudinal section through same. The holotype. Besom Farm Quarry. P.29721. × 1·5.

The left sensory field is faintly indicated and is seen to be narrow with a small postero-medial projection.

The ornamentation cannot be made out except around the naso-hypophysial aperture, as described, and along the margin where it consists also of minute reticulated ridges or tubercles.

REMARKS. This species is very clearly marked by the shape and size of the median dorsal sensory field alone. Both the previously described English species, *B. lankesteri* and *B. anglica*, as well as the three from the Red Bay Series of Spitsbergen have narrow dorsal fields, whereas the three from the later Wood Bay Series have wide fields, although not so large as that of *B. salopiensis* nor of the same shape (see Stensiö, 1932 : 152, pls. 47–49 ; text-figs. 55, 56 ; Wangsjö, 1952 : 446–467, pls. 68–75, text-figs. 77–84). This is in keeping with the high Dittonian age of these beds (see Westoll, 1951 : 12, table iii).

UNDETERMINED CEPHALASPID

A single fragment of a cephalaspid shield, measuring 1·0 × 0·75 cm. from Lower Ingardine Ford (P.33794), indicates the occurrence of another cephalaspid from these beds.

The specimen is partly in the form of an impression of the outer surface which shows the superficial layer divided by inter-areal canals and bearing numerous large, smooth, flattened, oblong tubercles, some over 1 mm. long. The basal layer is entirely lost and where the substance is preserved it shows the radiating canals with occasional casts of the ascending canals, etc.

The specimen most probably belongs to a species of *Cephalaspis* itself. Tuberculated fragments of this type have been obtained at Upper Overton Quarry (P.30079–80).

Order THELODONTI

An examination of the residue from the matrices of a few of the localities by Mr. H. A. Toombs has shown, surprisingly, that thelodonts were probably as widespread in these beds as they are in the lower series. So far only samples from Besom Farm Quarry, Upper Overton Quarry, Prescott Mill and Lower Ingardine Ford have been examined and minute scales have been found at each. The expectation now is that they will be found wherever residues are searched. A preliminary examination shows that scales resembling those of both *Thelodus* and *Lanarkia* were present, the scales being very similar to specimens described from the Upper Silurian Beyrichienkalk (Gross, 1947).

This is the latest occurrence of the group outside Spitsbergen. From North-west Spitsbergen Ørvig (1957 : 288) has recorded thelodont scales from various horizons in the Red Bay Series, and from the Kapp Kjeldsen Division of the Wood Bay Series, which may be comparable in age with the present series (Føyn & Heintz, 1943 : 47). Ørvig (1957) also describes and figures a number of scales, mostly with very large openings to the pulp-cavity, from the south end of Spitsbergen, which on still uncertain stratigraphical grounds, he considers to be even younger, possibly Middle Devonian.

Class GNATHOSTOMATA

Order ACANTHODII

That Acanthodian fishes, like the thelodonts, were present in numbers in these beds cannot be doubted. So far residues have yielded isolated scales at Besom Farm Quarry and Upper Overton Quarry. An asymmetrical carcharinid-like tooth of the *Plectrodus* type, 3·0 mm. high, a little more in length and less than 1 mm.

thick, with sharp cutting edges, also comes from the Besom Farm Quarry (P.28903; Pl. 45, fig. 3), along with five isolated spines of varying sizes. A sixth spine (P.29382) was found at The Gore, near Loughton Church. These six spines clearly show four or five different types of ribbing and probably belong to as many different species. That they do belong to Acanthodians and not to primitive sharks is a reasonable assumption on account of their age, in spite of their similarity in structure (Gross, 1940 : 7).

The spines are distinguished as follows :

(1) P.29082. 2·2 cm. long (slightly imperfect). Symmetrical. A very broad anterior median rib and four broad smooth lateral ribs in each side with narrow shallow grooves. With central cavity and shallow ventral groove, at least at tip.
(2) P.29083. 2·2 cm. long (slightly imperfect). Probably symmetrical. No median rib. Eleven or more sharp narrow smooth ribs divided by deep wide grooves. Large cavity.
(3) P.28887. Fragment 0·9 cm. long. Similar to (1).
(4) P.29081. Fragment of large spine, triangular in section, 2·7 cm. long and 0·8 cm. deep. Possibly asymmetrical. Large anterior median ribs and four widely and differently spaced, very smooth narrow ribs. Very large cavity.
(5) P.29089. 10 cm. long (almost complete). Rounded, no median rib, twelve or more appressed nodular ribs. Small cavity and open posterior groove.
(6) P.29382. Broken fragment 0·7 cm. long. ? Symmetrical. Broad anterior median rib with six moderately wide ribs and similar grooves. Large cavity. The Gore.

Nos. (1), (2), (4) and (5) are very distinct and clearly different from the other species described and have been named accordingly. No. (6), although different from the other spines is too fragmentary for description.

Genus ***ISCHNACANTHUS*** Powrie, 1864

Ischnacanthus (?) anglicus sp. nov.

(Pl. 45, fig. 4)

Diagnosis and description. This small slender spine now measures 2·2 cm. in length with about 0·2 cm. missing. It is straight and symmetrical except for a stepped fault near the base which from the local thickening of the ribbing is clearly due to damage healed during lifetime. It is attached along most of its hinder margin, except near the missing tip, which was free and shows a wide shallow posterior groove with no denticles and a circular central cavity, relatively small distally, but increasing posteriorly towards the open base. There is a broad, smooth and rounded median anterior ridge, on each side of which are four broad smooth ribs separated by deep and narrow grooves. The two posterior ribs are much narrower than the other two. The inserted portion is 0·4 cm. long and shows very fine ribbing. The line and angle of insertion was at about 45°, as shown by the line of demarcation. This, with its sharpness, suggests that it is a posterior dorsal or anal spine (cf. Watson, 1937 : 78, text-fig. 10).

HOLOTYPE. A small isolated fin-spine (P.29082, No. 1 above).

MATERIAL. In addition to the holotype a fragment of large spine (P.28887, No. 3); 0·9 cm. long.

LOCALITY. Besom Farm Quarry.

REMARKS. In spite of its simplicity of design, this little spine differs from its recorded contemporaries and has therefore been given a new specific name. It is perhaps nearest to *Onchus overathensis* Gross (*O. maior* Gross, 1933*a* : 65, pl. 5, fig. 9, text-fig. 11; 1937 : 67, pl. 8, fig. 8; text-fig. 29) but the anterior median ridge is wide and flatter and there are fewer lateral ribs. The general pattern agrees with that seen in *Ischnacanthus*, e.g. *I. gracilis*, (P.1344, P.6995, P.11165), and to that genus it is tentatively assigned.

Genus ***ONCHUS*** Agassiz, 1837

Onchus wheathillensis sp. nov.

(Pl. 45, fig. 5)

DIAGNOSIS AND DESCRIPTION. A small slender spine lacking both the tip and the inserted portion. As preserved it measures 2·2 cm. It is attached along its length by the back and right side. It has a large cavity, and is apparently symmetrical, i.e. a median fin-spine, and is slightly arched. The ribbing is narrow and sharp but smooth and the ribs are separated by deep and wide grooves. There is no continuous anterior median ridge but the foremost rib dichotomizes at intervals and on alternate sides, and this is also to be seen in the finer posterior lateral ribs. The largest number seen on the exposed surface is twelve but it may be still greater.

HOLOTYPE. A small isolated fin-spine (P.29083, No. 2 above). The only specimen.

LOCALITY. Besom Farm Quarry.

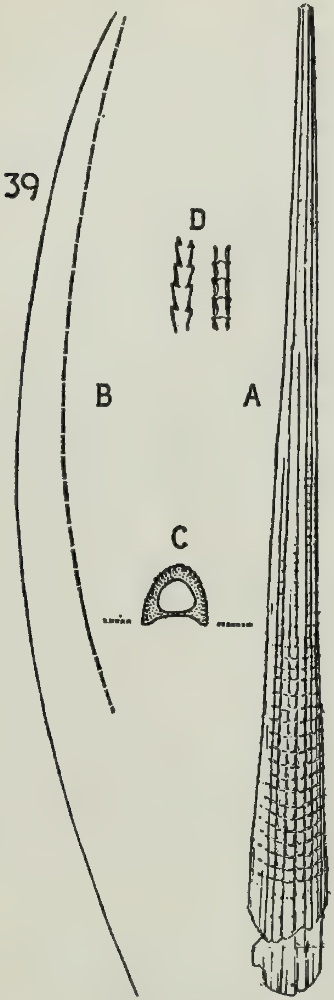
REMARKS. The ornamentation is not unlike that in some spines referred to *Onchus* but it is deeper and finer.

" Onchus " besomensis sp. nov.

(Text-fig. 38)

DIAGNOSIS. Large, triangular, laterally compressed, hollow spines with smooth sides decorated with four widely-spaced flat, narrow, smooth, longitudinal ridges, spaced 1 : 1 : 2 : 2 to anterior margin, which is acute distally.

HOLOTYPE. Fragment of large spine (P.29081, No. 4 above). The only specimen.



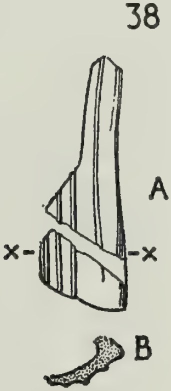


FIG. 38. *"Onchus" besomensis* sp. nov. Fragment of fin-spine. A, side view. B, cross-section at *x–x*. The holotype. Besom Farm Quarry. P.29081. × 1·3.

FIG. 39. *Nodonchus bambusifer* gen. et sp. nov. Dorsal fin-spine. A, anterior view. B, side profile. C, cross-section. D, ornamentation on ridges, further enlarged from the proximal end (left) and the middle. The holotype. Besom Farm Quarry. P.29089. A–C, × 1·3.

LOCALITY. Besom Farm Quarry.

DESCRIPTION. This fragment (Text-fig. 38) is 2·7 cm. long, but is no less than 0·8 cm. wide, and is probably from very near the base. The margin is slightly sigmoid, probably due to *post-mortem* distortion. It is acute distally, the two sides being at a little more than 45° to each other. There are four narrow, widely spaced ribs preserved and the end of a fifth forms the anterior edge for a short way, but then disappears running inwards towards the next rib, while the edge begins to broaden. The next rib becomes wider and broadens and also disappears before reaching the end of the fragment. It is separated from its neighbours by twice the distance between the next three.

The internal cavity is very large. Whether this spine belonged to a median or a paired fin is not clear. Judging by the relative sizes of Acanthodians and their spines, the fish was of the order of 30–50 cm. long.

Remarks. The low narrow ribbing and its arrangement on this large spine are characteristic and confusion with other known contemporary forms is not likely. It is referred to " *Onchus* " merely for convenience.

Genus ***NODONCHUS*** nov.

Diagnosis. Slender tapering spines gently arched with a single, large internal cavity and wide posterior groove apparently without marginal denticles; ornamentation of numerous rounded, closely noded ridges.

Type species. *Nodonchus bambusifer* sp. nov., the only species.

Nodonchus bambusifer sp. nov.

(Text-fig. 39)

Diagnosis. As for genus.

Holotype. Almost complete spine (P.29089, No. 5 above). The only specimen.

Locality. Besom Farm Quarry.

Description. The length of the spine, as preserved (Text-fig. 39) is 9·6 cm., but the extreme tip is missing, and the proximal end is so imperfect that the method of attachment is unknown. In the proximal region the spine is somewhat splayed but soon becomes more compressed laterally and tapers evenly to the distal end which has about one-fifth of the proximal breadth. The pronounced curvature is also even.

The surface is ribbed lengthwise with numerous ridges, over 30 in number near the proximal end, and finest on the sides where they gradually fuse in pairs as the breadth of the spine decreases, until less than a dozen are to be seen near the tip. These ribs are separated by deep but very narrow grooves, and are ornamented throughout with nodes, not unlike those on a bamboo (whence its trivial name). The nodes occur at short intervals which at first tend to get shorter distally but then increase somewhat towards the tip, in which direction the nodes themselves become fainter, while down the sides they become more and more oblique.

The posterior face is apparently in the form of a broad, shallow groove, the full width of the spine, and there are no flanking series of denticles on the one very short piece of margin that is preserved. Much of the posterior surface is broken open to show the very large internal cavity which continues throughout the length of the spine.

Remarks. Nodular ornamentation is recorded in *Climatius* (Gross, 1947 : 146, pl. 27, figs. 6–14 ; text-figs. 30, 31) among accepted Acanthodian genera and in a form-genus *Nodocosta* (Gross, 1940 : 13–14, pl. 1, figs. 8, 9 ; text-fig. 1F ; also as *Ctenacanthus*, Gross 1933*b* : 64, pl. 11, fig. 8). But in the former the spines are all less slender and the noding is only partial, while in both species of *Nodocosta* the spine is straight, certainly much shorter and more laterally compressed, and has a characteristic upper canal above the pulp-cavity. It seems safer to refer it to a form-genus of its own.

Order ARTHRODIRA

Remains of arctolepid arthrodires have been collected at ten localities in the Upper beds of the Clee area. Besom Farm Quarry, Prescott Reaside and Upper Overton Quarry have proved much the most prolific, and at these places the arthrodire remains are associated with those of both the pteraspids described above, *Pr. (E.) crenulata* and *Pt. (C.) leachi.*

Altogether there are some 50 specimens, but all are imperfect and most are the fragmentary isolated plates of small animals. All are ornamented with tubercles, the form and pattern of which is seldom distinctive, so that associating the fragments into species is most difficult, especially where two or more forms occur together as they clearly do at both Besom Farm Quarry and Prescott Reaside. It is, nevertheless, certain that at least six or seven species occur in these upper Dittonian deposits, and five are represented by characteristic and describable plates.

Only one is a known species, *Kujdanowiaspis anglica*, which unexpectedly survives from the earlier strata ; a second is a diminutive form of the same genus, based on a spinal plate. The other three species described are also largely based on single plates, but they present such peculiar features that each doubtless represents a new genus. One is a large anterior lateral with which nothing else can be associated, but type-specimens of the other two, like that of the new *Kujdanowiaspis* are small plates accompanied by numerous other specimens which are difficult to sort out among the species.

Genus ***KUJDANOWIASPIS*** Stensiö, 1942

Kujdanowiaspis anglica (Traquair)

(Text-figs. 40–43)

Material. Eight specimens, including parts of two anterior ventro-lateral plates, a scute and possibly part of a small skull-roof.

Localities. Besom Farm Quarry ; Prescott Reaside ; Newton Dingle 1 ; and Lower Ingardine Ford.

Description. Three specimens only are worth special attention.

The first specimen, from Besom Farm Quarry, is the imperfect impression with fragments of the plate of a right anterior ventro-lateral (P.28893 ; Text-fig. 40). It is a little distorted and lacks almost all the edges and the whole of the posterior outer quadrant. Nevertheless, in size and ornamentation it resembles the impression of the right anterior ventro-lateral plate described and figured upside down by

Woodward (1891 : 298, pl. 8, fig. 8), and the impression of three other specimens of the same part, all from the earlier beds at Heightington (Nos. 38032*c*, 37388*c* and P.16032). The ornamentation clearly comes within the range of variation in the species as now understood. As preserved, this plate is approximately 4 cm. square.

The second specimen is a small plate from Prescott Reaside, shown magnified in Text-fig. 41. Its maximum length is 1·0 cm. and breadth 0·7 cm., but the outline is peculiarly irregular, although apparently the specimen is complete. It is convex in both directions, with a well-marked, elongated, smooth, median spine projecting above the tubercular surface, the pattern of which is asymmetrical. The spine has a concave hinder margin. A very well-marked canal pierces the plate from below and seems to pierce the concave hinder margin of the spine on the upper surface. It is clearly a lateral line scale, and if correctly assigned to this form, the only one recorded. Similar but symmetrical and unpierced scales (presumably median ridge-scales) are known from Podolia (P.29222–23), while Denison (1958 : 482, text-fig. 93) has described such plates as " posterior dorsals " in the American genus *Aethaspis*.

The third specimen is the anterior end of a small skull-roof from Newton Dingle 1 measuring just over 2 cm. across the back of the orbits (Text-fig. 42). The ornamentation is very fine, finer than that on an even smaller specimen from Bryn Arw, near Abergavenny (Text-fig. 43). While its attribution is not certain, it probably comes within the wide limits of variation of this species.

The other fragments are of little account, except as distribution records.

REMARKS. These occurrences represent a considerable increase in the geological range of this species, and it is the only form known to be common to both upper and lower beds.

Kujdanowiaspis willsi sp. nov.

(Pl. 46, figs. 1, ? 2 ; Text-figs. 44, 45)

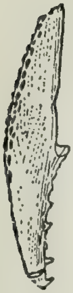
DIAGNOSIS. A small species of *Kujdanowiaspis* represented by a left spinal plate measuring 2·5 cm. in length, the attached and free parts being about equal. Rows of enlarged, elongated tubercles, arranged alternately along outer margin, about seven rows in front, the number decreasing to the rear, finally passing into a single continuous ridge. Denticles on inner free margin about seven in number, very large, recurved and thorn-like distally, well spaced and decreasing forwards in height to low bosses. Ornamentation on body of spine consisting of fine closely appressed oval tubercles, arranged more or less in longitudinal lines.

HOLOTYPE. A left spinal plate in counterpart (P.28913–14).

MATERIAL. Apart from the holotype some doubtfully associated specimens include a left central plate in counterpart (P.28889–90).

LOCALITY. Besom Farm Quarry.

DESCRIPTION. The spinal plate as preserved (Pl. 46, fig. 1 ; Text-figs. 44, 45) measures 2·5 cm. in length, with the distal end naturally fractured. There is still a little missing, the whole being originally about 3·0 cm. measured along the outer margin, of which about half is free spine. The outer margin is gently convex, the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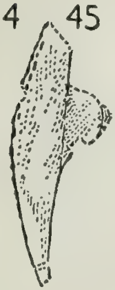
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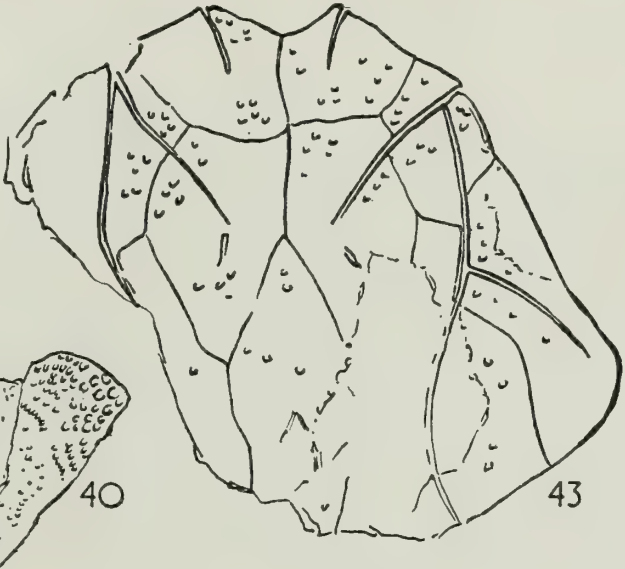
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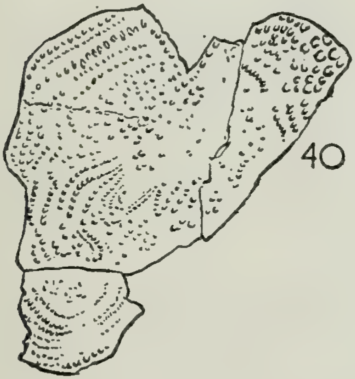
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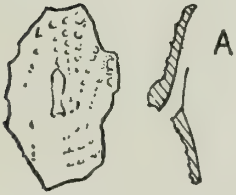

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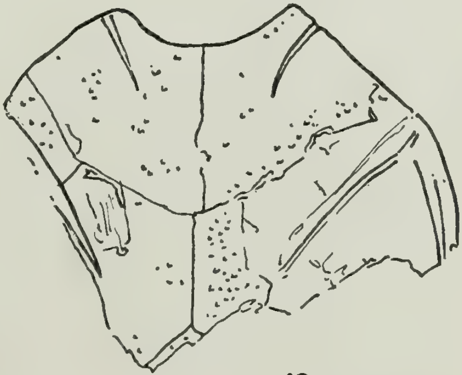
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Kujdanowiaspis anglica (Traquair)

FIG. 40. External impression of imperfect right anterior ventro-lateral plate. Besom Farm Quarry. P.28893. × 1·2.

FIG. 41. Lateral line scute,. A, longitudinal section. Prescott Reaside. P.29165–66. × 2·4.

FIG. 42. Anterior end of small skull-roof. Newton Dingle 1. P.29760. × 2·4.

FIG. 43. Imperfect small skull-roof. Bryn Arw, near Abergavenny. P.27190. × 2·4.

Kujdanowiaspis willsi sp. nov.

FIG. 44. Left spinal plate. The holotype. Besom Farm Quarry. P.28913. × 1·6.

FIG. 45. Counterpart of same specimen showing ventral surface. P.28914. × 1·6.

inner even more slightly concave and starting from a slight projection which is grooved to receive the lower posterior angle of the anterior lateral plate. Immediately in front of this lower projection the plate has its maximum breadth, 0·5 cm. The upper face is rather more convex than the undersurface. The latter is shown in the counterpart as an impression to which is attached part of the anterior ventro-lateral plate. Although their common margin is easily determined by slight differences in size and alignment of the ornament, these two plates are completely fused together, whereas the upper margin of the spine, to which the missing anterior lateral plate was attached, is rounded off. This piece of the anterior ventro-lateral plate is quite flat.

The spine on both surfaces is finely and closely tuberculated, the tubercles being low, smooth and oval, closely appressed and tending to run in lines roughly along the length of the spine. The narrow interspaces are usually slightly crinkled.

The tuberculations on the anterior ventro-lateral fragment are even finer and arranged in more definite lines running at an acute angle to those on the spine. The long outer margin of the latter bears along most of its length a number of rather indefinite rows of large elongated tubercles. The tubercles are closely spaced and generally alternate as between rows, of which there are seven or eight in front, but the number is gradually reduced towards the tip, near which the series is reduced to a simple continuous ridge. The individual tubercles are smooth, and the largest are 1 mm. long and 0·4 mm. wide.

On the mesial side of the spine is a row of conspicuous, widely spaced denticles. Distally they are relatively large and thorn-like, up to 1 mm. in height and about the same across the base, but they become lower and blunter towards the pectoral area where they disappear. There is evidence of seven on the spine but as the tip is missing, there were doubtless one or two more.

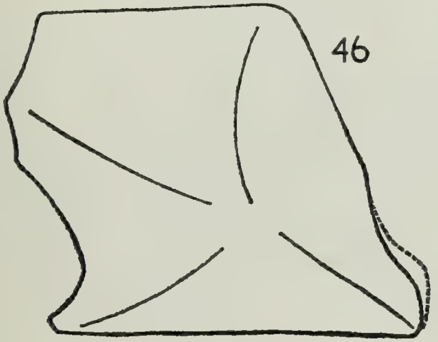
One other specimen from Besom Farm Quarry is very tentatively assigned to this species on account of some similarity of ornamentation. This is a left central plate, in counterpart (P.28889–90; Pl. 46, fig. 2). It is six-sided, although the truncation of the posterior angle may be an individual variation. Four of the sides, that is all but the anterior side and the short truncated end, are practically equal. The maximum length is 1·0 cm., the breadth, 0·75 cm. The surface shows the short end of the central sensory groove coming in from the front left side but there is no sign of the middle and posterior pit-lines.

The surface shows well the ornamentation especially in impression on the counterpart. The tubercles are smooth and rounder than in the holotype and the pores are more conspicuous. It is only here and there that the actual outer layer is preserved on the positive part, for otherwise an under layer of similar pattern but often on a smaller scale is shown.

REMARKS. This small species, named after Professor L. J. Wills who first drew the author's attention to the fauna, is distinguished from *K. anglica* by the generally finer ornamentation combined with relatively larger marginal rows on the spinal plate, and in the relatively large size of the spinal plate itself. Of two spinal plates in the Museum collection of the older species, one (P.16193) is a juvenile half the size of that of *K. willsi*, the other an adult (No. 37388*a*) four times as large, and in neither are the tubercles nearly so conspicuous or elongated. Moreover, in the small spine the free portion is only slightly greater than one-third of the total length, and the other, although lacking the tip, is proportionately stout.

Genus *OVERTONASPIS* nov.

Description. This new genus is based on a single large isolated right anterior lateral plate from Upper Overton Quarry (Pl. 45, fig. 6; Text-fig. 47), collected by Dr. H. W. Ball, after whom the type-species is named. Except for a notch along the upper margin and some cracks it is outwardly complete, but its inner face is defective, so that only the area overlapping the posterior dorso-lateral and posterior lateral plates are to be observed. It is 3·1 cm. in maximum height and a little under 4·0 cm. in breadth.



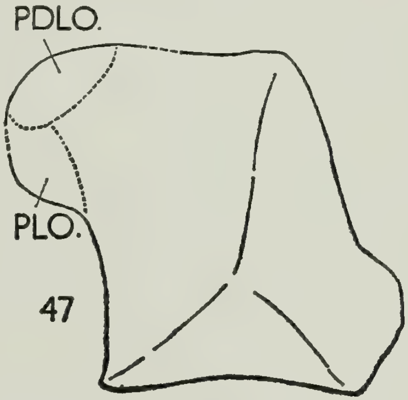


Fig. 46. Outline of internal impression of anterior lateral plate of *Kujdanowiaspis*. The broken line shows the shape of the apron when flattened. Podolia. P. 18241. × 1·5.

Fig. 47. Outline of anterior lateral plate of *Overtonaspis billballi* gen. et sp. nov. Upper Overton Quarry. P. 29272. × 1·5. *PDLO*, overlap of posterior dorso-lateral plate; *PLO*, overlap of posterior lateral plate.

Compared with the excellent outline restorations of comparable plates in other Arctolepids figured by Denison (1958 : 525, text-fig. 110) it is remarkable for the simplicity and squareness of its outline. The dorsal and ventral margins, both slightly emarginate, are roughly parallel, but more noteworthy still is that the upper half of the slightly inturned apron is parallel with the vertical lower half of the hinder margin which borders the pectoral fenestra. The upper part of the posterior margin starts at right angles to the lower and is almost semicircular. The lower half of the anterior margin forms a blunt angle approximately on a level with the centre of ossification, which is 0·8 cm. from the ventral margin and 1·3 cm. from the hinder margin. The exposed surface is divisible into three very unequal areas which meet at the centre of ossification. The largest area, comprising most of the surface, is separated from the apron in front by a line marked by an abrupt change in ornament and a less obvious change in plane running from the top anterior corner to the centre of ossification ; and from the basal area by a slight ridge with change in tuberculation running from the centre of ossification to the rectangular posterior lower corner. The apron and the basal area are separated by a low rounded ridge leading from the centre of ossification to the obtuse anterior lower corner, so that the basal area is almost a low isosceles triangle.

The apron gently slants inwards, especially the lower part which is also slightly hollow, while the basal area is slightly concave, the bottom margin of the plate being incurved. Curiously the whole of the main area is somewhat concave and markedly so in the rounded dorso-posterior area, where the margins are definitely outwardly turned. The extent to which this is due to distortion is not clear, but it is not entirely so.

The ornamentation is very distinctive. It is, as is generally the case, tubercular, but the tubercles are absolutely smooth, and so, as a rule, are the interspaces. The largest tubercles are pointed and mammiform, and arranged roughly in rows parallel with, and near to, the dorsal and posterior margins. They gradually decrease in size towards the centre of ossification. On the basal area and the upper part of the apron the tubercles are almost granular, but on the lower, wider part of the apron they are somewhat larger and triangular with the apices pointing downwards and outwards, exactly as in *Williamsaspis* (White, 1952 : 265, pl. 28, fig. 1).

A fragment 1·5 cm. long (P.29274) from the same locality shows similar but small smooth denticles.

DIAGNOSIS. The genus is temporarily defined as including Arctolepids of moderate size in which the anterior lateral plates have approximately parallel upper and lower borders with the lower hinder and upper front borders at right angles in direction, the upper half of the hinder border being in the form of a semicircular projection, the lower front, obtusely angular. Ornamentation tubercular, the tubercles and interspaces being quite smooth, and the largest tubercles, on the upper hinder projection being long and mammiform.

TYPE SPECIES. *Overtonaspis billballi* sp. nov., the only species.

Overtonaspis billballi sp. nov.

(Pl. 45, fig. 6 ; Text-fig. 47)

DIAGNOSIS. As for genus.

HOLOTYPE. A right anterior lateral plate (P.29272), the only specimen.

LOCALITY. Upper Overton Quarry.

Genus ***PRESCOTTASPIS*** nov.

DESCRIPTION. This genus is based on a small posterior lateral plate (Text-fig. 48) from Prescott Reaside with which are associated ten or a dozen fragments from the same locality, but of these only three, part of a left posterior dorso-lateral plate

(P.29153), an even smaller piece of a right posterior ventro-lateral, and a scute are worth description. Obviously the association of such small fragmentary plates can only be tentative but constructional features seem to tie the plates mentioned together. A left posterior ventro-lateral plate without ornament is also described here.

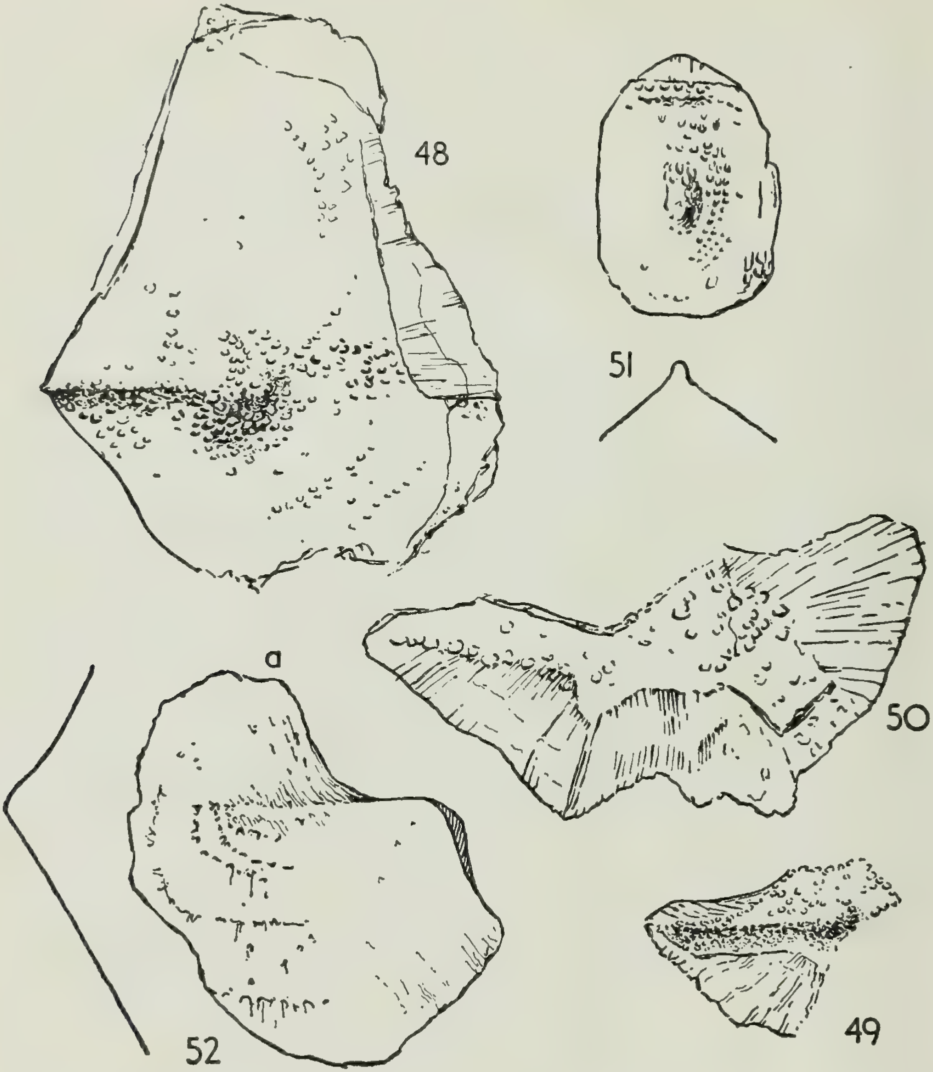
The posterior lateral plate, from the right side, is most remarkable (Text-fig. 48) and quite unlike any other comparable plate (cf. Denison, 1958 : 526, text-fig. 111), with the exception of that of *Williamsaspis* (White, 1952 : 259, pl. 26, fig. 2 ; pl. 27, fig. 2 ; text-figs. 7, 11) which it resembles in that its height (1·5 cm.) exceeds its maximum length or width (1·2 cm.). The latter occurs 1 cm. from the short (0·5 cm.) and somewhat convex dorsal margin. From the top the two sides slope gently outwards, the posterior gently concave and grooved (presumably for attachment of the skin), and the anterior irregularly sigmoid and marked by a right-angled area of overlap. This finishes in a short, deep groove at the maximum breadth, which is marked behind by a point rather larger than a right angle. From this posterior angle a conspicuous and undercut ridge runs forward and passes into a well-marked boss towards the middle of the plate. The lower part of the plate is certainly imperfect, for it lacks the posterior ventro-lateral overlap. As preserved it is nearly semicircular. The angle between the lower and upper parts is small, about 10°. The ornamentation consists of rather conical, slightly fluted tubercles with the usual wrinkled interspaces and pores.

Associated by reason of the similarity of the ornament is a fragment consisting of the ventral median extension of a right posterior ventro-lateral plate (Text-fig. 49). It measures 0·7 cm. in length with a maximum breadth of 0·45 cm., of which half is occupied by the area overlapped by the left plate. This is the usual overlap, but it must have been relatively very large indeed—again after the style of *Williamsaspis*. The upper free margin is concave. Like the first specimen this plate has a sharp ridge dividing the ventral and lateral surfaces, which passes forwards into a boss.

Much less certain in its attribution to this genus is a nearly complete left posterior ventro-lateral plate (Pl. 46, fig. 4 ; Text-fig. 52). It is 1·1 cm. in height with a maximum width of rather less than 1 cm. The whole of the ornament has disappeared and the surface is smooth save for structural features. The wide ventral part is divided from the small lateral flange by a pronounced ridge, not unlike that of the two previous plates, but the association is very tentative.

More confidently attributed to this form is a left posterior dorso-lateral plate of which the dorsal part has been destroyed (Text-fig. 50). The lower margin, with deep areas overlapped by the two lateral plates, is intact and so is the supposedly posterior margin, but the external ornamented layer has been removed from the hinder region. It is peculiar in having a substantially longer overlapped area for the anterior lateral plate than for the posterior (cf. Denison, 1958 : 522, text-fig. 109), but that the plate is properly identified and orientated is confirmed by the narrow upper end of the first plate described, the upper end of which fits admirably the hinder area.

The outer surface is much mutilated except for a strip immediately above the



Prescottaspis dineleyi gen. et sp. nov.

FIG. 48. Right posterior lateral plate. The holotype. P. 29152. × 5.

FIG. 49. Fragmentary right posterior ventro-lateral plate. P. 29156. × 4·8.

FIG. 50. Fragmentary left posterior dorso-lateral plate, possibly of this species. P. 29153. × 4·8.

FIG. 51. Median body-scute with cross-profile below. P. 29267. × 5·2.

FIG. 52. Imperfect left posterior ventro-lateral plate without surface ornament, possibly of this species, with cross-profile at A. P. 29259. × 4·8.

All from Prescott Reaside.

overlapped areas. The ornament is tubercular but coarser and more worn than in the two preceding plates. There is no indication of the lateral line.

The last specimen is of great interest, for it is a median body-scute (Pl. 46, fig. 3; Text-fig. 51). It is bowed from side to side with slightly convex sides, which are, however, imperfect, and has roughly straight posterior and anterior margins. In front there is also a triangular overlapped area, showing that it was one of a continuous series. Whether it overlapped in turn a scale behind it is not clear. There is a low but well-marked median spine. It is uncertain whether it belonged to a dorsal or ventral series. The overall length is 7 cm. and the maximum breadth 4·5 cm. Attention has already been drawn to median body-scutes in the case of *Kujdanowiaspis* above (p. 290).

The ornamentation is very well preserved, consisting of small conical denticles varying in size according to position. Most lean backwards and all show the flutings seen in the previous specimens.

The other specimens from Prescott are doubtful fragments and show little else than indifferently preserved ornamentation.

REMARKS. The genus may be defined on the form of the posterior lateral plate, which is most distinctive and clearly shows that the form belongs to at least a family of its own, the Prescottaspidae. Among the other arthrodires from these beds, the ornamentation, with its fluted conical tubercles, is easily distinguished when fresh.

TYPE SPECIES. *Prescottaspis dineleyi* sp. nov., the only species.

Prescottaspis dineleyi sp. nov.

(Pl. 46, figs. 3, ? 4; Text-figs. 48–52)

DIAGNOSIS. As for genus.

HOLOTYPE. A right posterior lateral plate (P.29152).

MATERIAL. In addition to the holotype, part of a right posterior ventro-lateral plate (P.29156), an imperfect left posterior dorso-lateral plate (P.29153) and a median scute (P.29267) and some fragments.

LOCALITY. Prescott Reaside.

Genus ***WHEATHILLASPIS*** nov.

DESCRIPTION. A fourth genus of arctolepid is represented by a small and imperfect anterior ventro-lateral plate with part of the spinal plate attached, from Besom Farm Quarry (Pl. 46, fig. 5; Text-fig. 53). The anterior margin and part of the inner margin are missing, likewise the tip of the spine. The maximum width of the combined plates is 2·0 cm. The most striking feature is the great size of the pectoral fenestra (*P.F.*) which occupies more than three-quarters of the outer margin of the anterior ventro-lateral plate, from the contact with the spinal plate to the short dorsal extension (*D.E.*). This fenestral margin, to which fragments of the perichondral bone of the scapulo-coracoid are attached, is concave bow-shaped with a blunt middle prominence, the whole lying about 45° to the length of the fish. The dorsal extension behind it was narrow, occupying about half the remainder of this outer margin. How high it extended cannot be judged, but presumably it overlapped the posterior ventro-lateral plate in the manner of Stensiö's (1944 : 60, text-fig. 17) restoration of *Kujdanowiaspis*. The posterior margin shows an obtuse angle dividing a short straight outer border from the larger bowed medial border, which passes into the inner margin.

The spinal plate is not clearly marked off from the anterior ventro-lateral but the division can be detected below the anterior end of the pectoral fenestra. It was broad and probably moderately short. The outer margin bears two or more rows of enlarged, well-separated rounded tubercles, but there are no signs of denticles on the inner margin as preserved. The ornamentation on the plates is tubercular, the tubercles being round and generally fine but mixed with even finer papillae with patches here and there of larger tubercles. In a few areas where wear has been less than usual, the tubercles are seen to be faintly striated or fluted.

Two other small plates from Besom Farm Quarry are tentatively associated with the foregoing, chiefly on the grounds of similarity in ornamentation.

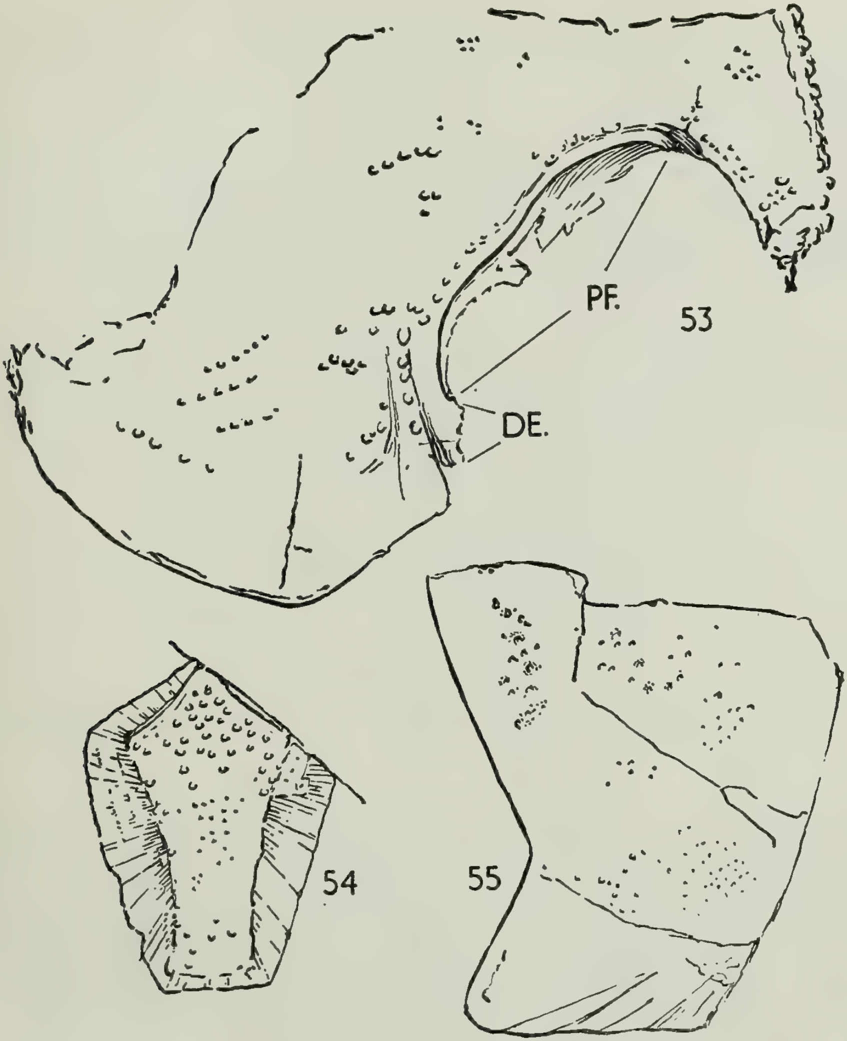
The first is a median ventral plate (Text-fig. 54). It is coffin-shaped, 1 cm. in length and about 0·75 cm. across at its maximum. The lateral overlapped areas are wide and the borders of the ornamented surface gently concave, and so is the supposed right anterior border where the overlap was increasingly narrow (the left is partly cut away). The narrow posterior margin is either straight or gently convex, and there is apparently a very narrow overlapped selvage which, however, may be due to imperfect preservation. The ornamentation is a mixture of fine or very fine rounded tubercles, which occasionally show signs of fluting. The plate is described as an anterior median-ventral, after the style of *Bryantolepis* (Denison, 1958, 533, text-fig. 113) rather than as a posterior plate like that of *Phlyctaenaspis* or *Prosphymaspis* (Gross, 1937 : 21, text-fig. 12), but there is no evidence one way or the other.

The second plate, doubtfully referred to this form is an imperfect left anterior lateral (Text-fig. 55). The apron in front is entirely missing and so is the dorsal border. As preserved, the plate measures 1·4 cm. in height with a maximum breadth, along the top, of 1·2 cm. The outstanding feature is the simple angularity of the hinder margin, and the obtuseness of the rounded postero-inferior angle. It is to be matched in none of the plates outlined by Denison (1958 : 525, text-fig. 10).

The lower third shows the inner surface, which is much grooved towards the centre of ossification, but the remainder is preserved as an external impression. The ornamentation is finely but variably tubercular, the finest tubercles being towards the lower front and the largest in the top back segments.

The tubercles are well separated with the intervening spaces crinkled or papillated. The smallest are round but become more and more oval with increase in size, and the largest show marked flutings. This ornament comes well within possible variation for the genus and species.

An imperfect right anterior ventro-lateral plate from Upper Overton Quarry (P.30087) may belong to this genus and species, but the critical fenestral margin is too imperfect for certainty. There is also a worn, almost symmetrical scute (P.30086).



Wheathillaspis wickhamkingi gen. et sp. nov.

FIG. 53. Part of left anterior ventro-lateral and spinal plates. *DE*, dorsal extension of anterior ventro-lateral plate; *PF*, pectoral fenestra. The holotype. P.28908. × 5·6.
FIG. 54. Median ventral plate. P.28910. × 4·8.
FIG. 55. Imperfect left anterior lateral plate, largely in impression. P.28911. × 4·8.
All from Besom Farm Quarry.

REMARKS. The genus is best defined on the basis of the first specimen, the essential features being the very large, oblique pectoral fenestra (cf. Denison, 1958 : 530, text-fig. 12).

TYPE SPECIES. *Wheathillaspis wickhamkingi* sp. nov., the only species.

Wheathillaspis wickhamkingi sp. nov.

(Pl. 46, fig. 5; Text-figs. 53–55)

Diagnosis. As for genus.

Holotype. An imperfect left anterior ventro-lateral plate with part of spine (P.28908).

Material. Apart from the holotype there is a median ventral plate (P.28910), an imperfect left anterior lateral plate (P.28911–12) and more doubtfully still, an imperfect right anterior ventro-lateral plate (P.30087), and a scute (P.30086).

Localities. Besom Farm Quarry; ? Upper Overton Quarry.

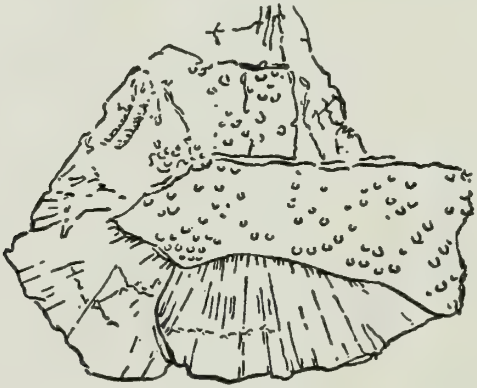


Fig. 56. Gen. et sp. indet. Fragmentary left posterior dorso-lateral plate. Stottesdon Brook. P.28353–54. × 4·8.

UNDETERMINED ARCTOLEPIDS

Among the material that cannot be assigned clearly to one of the species described are two interesting plates worthy of some attention.

Text-fig. 56 shows an imperfect posterior dorso-lateral plate from the left side, from Stottesdon Brook, the only arthrodire fragment from the locality. It is 1·2 cm. in length, but the depth is uncertain for almost all the plate above the lateral line is damaged. The lower part is intact and shows, in contrast to the same plate of *Prescottaspis* (Text-fig. 50), a narrow anterior overlap for the anterior lateral plate. This is normal for the group (see Denison, 1958 : 522, text-fig. 109), but in its imperfect state it does not bear any striking resemblance to the forms figured. Allowing for variation in the species and individuals it comes nearest to the plate in *Kujdanowiaspis* (see Stensiö, 1944 : 60, text-fig. 17A). The tuberculations are of the usual stellate form seen in that genus.

The other specimen of particular interest is a stout, very asymmetrical plate, which clearly seems to be a body-scute, from Upper Overton Quarry (P.29756, Pl. 46, fig. 6). It is an extremely thick plate much wider than deep. The long sides are roughly parallel but the upper is slightly convex and shorter than the lower, which is concave, the length being 1·4 and 1·6 cm. respectively. The depth is 1·0 cm. The anterior end (right of figure) is unevenly sigmoid with a short embayment at the top ; the straight truncation of the convex lower part is artificial. The hinder end is gently convex but broken by a most conspicuous ridge or blunt spine. This striking feature is deeply undercut behind, but above the slope upward is flat and the whole disappears gradually forwards. The ornament is of relatively corase tubercles with crinkled bases arranged roughly parallel with the sides, very much like that in *Kujdanowiaspis anglica*. It may indeed belong to that species, but similar plates have not been recorded elsewhere. The only other specimen of an arthrodire plate from this locality is the anterior lateral of *Overtonaspis*, which has very different ornamentation.

III. FAUNA OF THE FARLOW SANDSTONE SERIES

Only six localities in the Upper Old Red Sandstone of the Clee area have yielded fossils, three being in the Yellow Farlow Sandstone Formation at Prescott Corner, Farlow, Old Lane, and the old Church Quarry, near Farlow, the exact situation of which is not now known but which was probably in Farlow Bank, a little to the north of the church for the building of which it was opened. The Prescott material, from a roadside section, is extremely fragmentary, but it can be related to the more extensive material from Church Quarry from which Woodward (1891 : 231, 249, 366) recorded *Bothriolepis macrocephala*, ? *Phaneropleuron* and *Sauripterus anglicus*. The fragments yielded by the three localities in the Grey Farlow Sandstone Formation at Prescott, Old Lane and Walton Brook 1 and 2, are very poor.

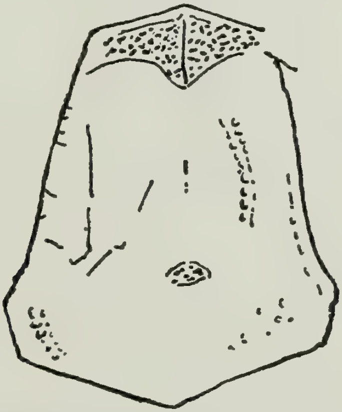


FIG. 57. *Bothriolepis* cf. *hydrophila* (Agassiz). Imperfect posterior median dorsal plate. Church Quarry, Farlow. P.27167. × 1·5.

Class GNATHOSTOMATA

Order ANTIARCHI

Genus ***BOTHRIOLEPIS*** Eichwald, 1840

Bothriolepis macrocephala Egerton

Both A. S. Woodward (1891 : 231) and Stensiö (1948 : 511) have suggested that this species was related to *B. hydrophila* (Agassiz), either as a variety or as the young, but no specimens of a larger species were recorded from Church Quarry, Farlow, the only locality from which *B. macrocephala* was known. Curiously enough, there was in the collection at that time, a very fair posterior median dorsal plate that, in its shape, might very well belong to *B. hydrophila* (Text-fig. 57); and now at Prescott Corner fragmentary remains also of a large species, unfortunately too incomplete for identification, have been found associated with very small isolated anterior and posterior median dorsal plates only 6 to 8 mm. in length. It seems probable that this species is based on the young of the larger species, but the identity of the larger species cannot be established for certain; and although it may be *B. hydrophila*, the ornamentation on the larger plates is retiform rather than nodular, as in other species, and so *B. macrocephala* may be distinct, although attaining a much larger size than had been supposed.

Order CROSSOPTERYGII

Family Holoptychiidae

Genus ***PSEUDOSAURIPTERUS*** nov.

Sauripterus anglicus was described by A. S. Woodward (1891 : 366, pl. 16, figs. 4–6) from two slabs, each showing a number of isolated scales (P.200, P.200*a*), and one a laniary tooth; a large isolated scale (P.200*b*) and the impression of an isolated tooth (P.201) which was in fact the counterpart of the tooth on the type slab (P.200). There are a number of other specimens not described. All are from Church Quarry, Farlow and came to the Museum in the Weaver-Jones Collection in 1880. Part of the counterpart of the type slab was acquired with the collection of the Rev. P. B. Brodie in 1895. The scales were described by Woodward as " robust, the exposed portion ornamented with coarse, sparsely and irregularly arranged tubercles ", but of the figured scales from the type slab pl. 16, fig. 6 shows only the broken middle layers and the other (pl. 16, fig. 5) the undersurface. Part of the type slab and the whole of the counterpart and the second slab have been etched in hydrochloric acid to remove the broken middle layers, leaving very clear impressions of both upper and lower surfaces (Pl. 47, figs. 2–5), which show that the supposed external ornament of tubercles are tubercles pierced by pores on the undersurface of the scale; while the true ornament of the exposed area of the upper surface is seen to consist of fine simple ridges, running lengthwise across the scale, but fading out before reaching the hinder margin. The ridges are generally well separated and roughly parallel with one another, although occasionally meeting, and in some of the scales from Prescott Corner are broken into short lengths (P.28967). On the relatively coarse matrix only occasionally can fine transverse wrinkles be detected (P.27173) in the valleys between. Behind the ridges on the overlapped portion of the scale are short radiating lines of tubercles, usually dimpled (P.27172), as in *Glyptolepis* (cf. Jarvik, 1950 : 111, text-fig. 33; Ørvig, 1957 : 386, text-fig. 4).

Several of the scales show on the upper surface the external branches of the lateral line, which can be seen on each scale just behind the radiating tubercles on the overlapped area as broad, rapidly deepening grooves that disappear below the surface at the beginning of the exposed area, at the same time giving off six or more shallow radiating canals (seen in the photographs, Pl. 47, figs. 2, 4 as narrow grooves) that sometimes branch still further, the canals ending as well-separated pores on the exposed surface of the scale near the hinder margin. In two scales (one each on P.200*a* and P.7601) the undersurface shows the corresponding exit of the main canal near the hinder margin where it runs backwards and downwards on to the scale it overlaps. A similar, but rather coarser, arrangement can be seen in a single scale of a specimen (No. 41413) of *Glyptolepis leptopterus*, but the groove of the main canal seems longer and deeper.

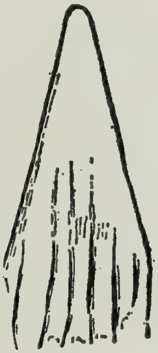


FIG. 58. Impression of Crossopterygian tooth, counterpart of specimen described and figured as *Sauripterus anglicus* by A. S. Woodward, 1891 : 366, pl. 16, fig. 4. P.201. × 3.

Some of the scales are over 3·0 cm. high and if in proportion to those of *G. leptopterus* would indicate a fish about 120 cm. in length.

Woodward referred this species tentatively to the same genus as the American *Sauripteris* (usually written *Sauripterus*) *taylori* Hall but the scales of that fish, of which three[1] are figured on Plate 48, are very differently ornamented. In any case *Sauripteris* is a Rhizodont, whereas the radiating lines of tubercles on the overlapped part of the scales shown in this fish are deemed by Ørvig (1957 : 391) to be the hall-mark of a Holyptychiid. The new genus *Pseudosauripterus* differs from *Glyptolepis* in respect of its scales to the same degree that the latter differs from *Holoptychius*, in the still finer and simpler nature of the ornament on the exposed surface, and may be defined briefly as follows : Holoptychiid fishes in which the external ornament of the scales consists of fine simple ridges running lengthwise across the scale but disappearing before reaching the hinder border, well separated and roughly parallel with one another but sometimes anastomosing and in some cases broken up into short lengths.

Type and only known species, *Sauripterus anglicus* A. S. Woodward.

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[1] For these I am indebted to Dr. Bobb Schaeffer, of the American Museum of Natural History, N.Y.

There are several more fragmentary pieces from Prescott Corner, of which the best is an imperfect cleithrum and clavicle (P.32256).

The associated tooth on the type slab (P.200), which is 1·6 cm. high, 0·7 cm. across the base and split down the middle, was figured by A. S. Woodward (1891, pl. 16, fig. 4) and described as " straight and regularly tapering, moderately compressed ". The counterpart, an external impression (Text-fig. 58) shows the tooth to be very little compressed, and perfectly smooth in the upper half. There are about fourteen deep basal vertical grooves which almost disappear about 0·6 cm. height but which are in fact continued faintly, at first with subsidiary grooves, for some distance before finally disappearing. The wide conical cavity is seen up to 0·9 cm. This tooth has a rather Rhizodont aspect and its reference to this species is questionable.

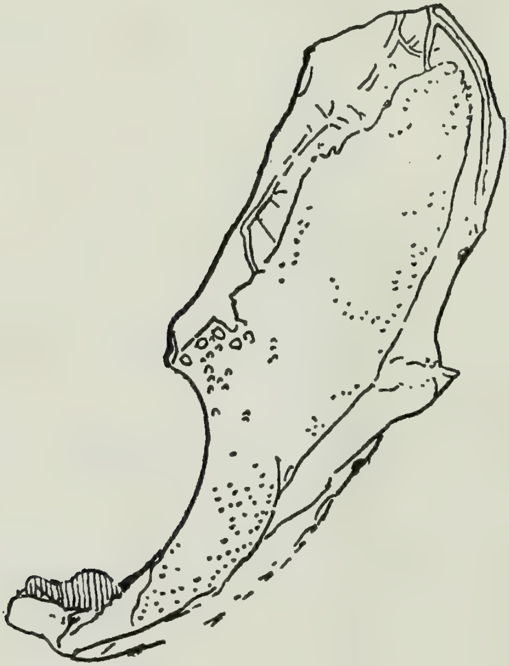

FIG. 59. *Pseudosauripterus anglicus* (A. S. Woodward). Cast of right entopterygoid referred to this species. Church Quarry, Farlow. (See Pl. 47, fig. 1.) P.27176. × 1·5.

From the same collection and locality as the type scales and the tooth comes a most interesting specimen not mentioned by Woodward. This is a right entopterygoid, now an external impression, in counterpart (Pl. 47, fig. 1; Text-fig. 59). It seems likely to belong to this fish but there is no comparable material of this family for comparison. The palatine region is wide and the quadrate part a long narrow curved bar, the smooth outer margin of which bordered the wide adductor fenestra, ending in an expansion for the support of the quadrate articulation. The medial or upper border shows a wide overlapped area for seating the palato-quadrate complex, with a triangular ascending process. This area continues in front and then below, for the ectopterygoid, dermopalatine and possibly vomer, showing a rather irregular inner margin. On both upper and lower overlapped borders are wide grooves for branches, presumably of the palatine artery. The whole exposed surface of the bone almost to the hinder end of the bar is covered with fine sharp teeth which increase considerably in size just in front of the outer border of the adductor fenestra. This bone is quite unlike the corresponding element in *Eusthenopteron* (Jarvik, 1954, text-figs. 16, 25) in its slender quadrate ramus and consequently in the shape of the dentigerous area, in both of which it rather strikingly resembles the ichthyostegid *Ichthyostegopsis wimani* Säve-Söderbergh (1932 : 69, pl. 17, fig. 2 ; text-fig. 13) and to a less extent the Rhizodont *Eusthenodon* (Jarvik, 1952 : 66, pl. 16, fig. 2 ; text-fig. 29). On the other hand the upper overlapped margins indicate some agreement with *Megalichthys* and *Eusthenopteron* as figured by Watson (1925 : 247, text-figs. 32–34) with " a series of supra-pterygoid ossicles ", of which the quadrate in *Pseudosauripterus* lies in a long groove ending in an expansion at the articular end. The middle and hinder part of this overlapped area is bent upwards at a considerable angle to the dentigerous area and must have stood almost vertically in the head.

Two very imperfect cleithra (P.28999, P.32256) from Prescott Corner may belong to this species. They show very similar ornament to that in *Glyptolepis leptopterus* (Jarvik, 1949 : 30, text-fig. 9*a*). One shows part of the endoskeletal girdle.

Pseudosauripterus anglicus (A. S. Woodward)

(Pl. 47 ; Text-figs. 58, 59)

DIAGNOSIS. As for genus (only species).

TYPE SPECIMEN. Slab with about a dozen scales and a tooth, partly in impression (P.200), in part counterpart (P.7601, P.201), from Church Quarry, Farlow. The species is based on the scales, of which that figured by A. S. Woodward (1891, pl. 16, fig. 6—see also Pl. 47, fig. 5 of this work) is chosen as lectotype.

LOCALITIES. Church Quarry, Farlow and Prescott Corner.

Family RHIZODONTIDAE

Genus ***EUSTHENOPTERON*** Whiteaves, 1881

Eusthenopteron farloviensis sp. nov.

(Text-fig. 60)

DIAGNOSIS. An *Eusthenopteron* distinguished by the shape of the cleithrum.

HOLOTYPE. Scattered remains on slab, most probably from Church Quarry, Farlow (P.43444).

MATERIAL. In addition to the holotype, two scales from Church Quarry, Farlow (P.27165–6) and a scale (P.28979) with a few doubtful fragments of plates from Prescott Corner.

Description. The holotype is a large slab of yellow sandstone, unlocalized but identical in matrix with those from Farlow, which shows the remains of a medium-sized fish. It includes numerous scales, the anterior part of the tail, part of the vertebral column and the left cleithrum.

The cleithrum (Text-fig. 60) is almost complete, having lost only a little of its dorsal border, and the anterior ventral margin, where it is overlapped by the clavicle, is slightly compressed. It is 8·0 cm. high and has a breadth of 2·5 cm. which does not vary more than 2 mm. from one end to the other and it is not divided clearly into dorsal and ventral parts as in the type species *E. foordi* (cf. Text-fig. 61 ; Jarvik, 1944*b* : 12, text-figs. 3D, 4D), and the posterior margin is almost straight without the " heel " shown in the Canadian species. Moreover, the process of the cleithrum at the top of the border along the overlap of the clavicle is large and the ventromedian projection less developed.

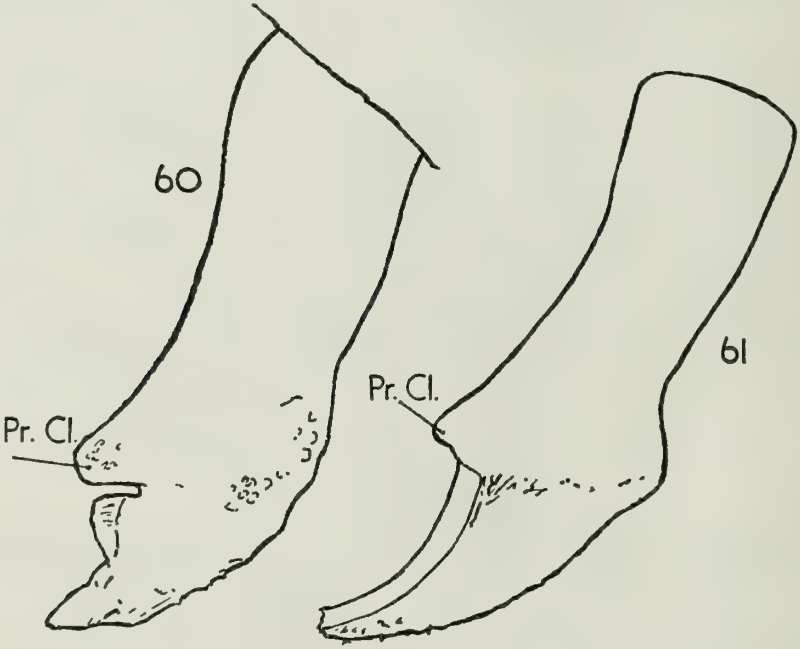

Fig. 60. *Eusthenopteron farloviensis* sp. nov. The left cleithrum. *Pr. Cl.* process of cleithrum. The holotype. [Church Quarry, Farlow.] P.43444. × 1.

Fig. 61. *Eusthenopteron foordi* Whiteaves. The right cleithrum (reversed). *Pr. Cl*, process of cleithrum. Scaumenac Bay, P.Q., Canada. P.6797, P.6797*a*. × 1.

On the other hand the ornamentation, so far as it can be determined, is the same as in *E. foordi* as shown in P.6797*a*, consisting of vermiculating ridges which become very tubercular on the ventral face, which in life was bent horizontally underneath the fish. This tubercular development is not shown in Jarvik's figures.

There are about 80 cycloid scales, mostly preserved as external impressions. They vary in size from 1·5 × 1·3 cm. to 0·9 × 1·2 cm. The ornament, as in *E.*

foordi, consists of between 16–22 well defined parallel longitudinal ridges and is very different from that seen in *Tristichopterus*, in which the ridges tend to run with the margins of the scales and thus converge along the mid-line (Nos. 42398, 42406). Several scales on the new specimens show the Rhizodont boss on the underside. Two similar scales are in the original collection from Church Quarry, Farlow (P.27165–6).

The remains of the axial skeleton are confined to the neural and haemal spines of the tail region, the whole closely resembling those of *E. foordi.*

The cleithrum and the scales are only slightly bigger than those of specimen P.6797, which has a head-length of 17·5 cm. and would therefore have belonged to a fish of about 80 cm. in total length.

The only other specimens that may belong to this species is a fragmentary impression of a jaw-bone with teeth (P.28965–66) from Prescott Corner, which, with a scale, have already been recorded as *Eusthenopteron* sp. by Ball & Dineley (1952 : 213).

REMARKS. Five species have been referred to *Eusthenopteron*, *E. foordi* Whiteaves from Canada, *E. traquairi* Westoll from Boghole, Scotland, *E. säve-söderberghi* Jarvik from Livonia and *E. wenjukovi* (Rohon) from Russia, with a fifth, *E.* ? *dalgleisiensis* (Anderson), from Dura Den tentatively added to the list. Of these only in *E. foordi* and *E.* ? *dalgleisiensis* is the shoulder-girdle known and comparison has already been made with *E. foordi* to establish sufficient distinction, while in *E.* ? *dalgleisiensis* the rounded form of the cleithrum is even more distinctive (Jarvik, 1950*a* : 28, text-fig. 9A). With the other three species known only by remains of the head no comparison can be made. They, like *E. foordi,* are from beds near the base of the Upper Old Red Sandstone (Westoll, 1937 : 522), but the range of the genus is substantially increased upwards if *E.* ? *dalgleisiensis* is correctly assigned to this genus (Westoll, 1951 : 12, Table III), since Dura Den is considered to be of Middle Famennien age (Jarvik, 1950*a* : 33).

Order DIPNOI

Genus Indet.

The " impression of a small dental plate (P.198) with five coarsely tuberculated ridges " from Farlow referred by Woodward (1891 : 249, No. P.198) " to *Phaneropleuron* with much probability of correctness " is not clear in its definition. There are indications of a sixth ridge and it might as well be the plate of a dipterine.

IV. ACKNOWLEDGEMENTS

The palaeontological section of this work was in the first place planned merely as an appendix providing information for the main stratigraphical memoir of Drs. Ball and Dineley ; but like Topsy, it " growed and growed ", until it has had to be accorded an almost independent status. Its main purpose is still to serve the stratigraphers, and to that end and under the inexorable pressure of diminishing time, it has been largely restricted to a systematic study of the material provided.

It is to be hoped that in the hurry the servant has not left too much dust under the stratal carpet ; and he is grateful that his tardiness, not entirely the result of inevitable senescence, has been borne with patience.

Discussion with Professor D. M. S. Watson has had its usual fruitful results ; Mr. H. A. Toombs has shown his wonted skill in the preparation of many refractory specimens ; and Mr. R. Baker his customary deftness in converting an almost illegible MS. into an orderly typescript on which Mr. F. M. Wonnacott has exercised his habitual discretion as editor ; and finally Mr. Philip Gurr, during his ephemeral association with the Department, has achieved a welcome degree of excellence in his preparation of the plates ; to all I gratefully acknowledge my indebtedness.

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PLATE 33

Pteraspis (*Pteraspis*) *dairydinglensis* sp. nov.

FIG. 1. Uncrushed rostral region. Hopton Brook 4, Hopton Wafers. P.42360. × 2.

FIG. 2. Imperfect dorsal shield. Hopton Brook 4, Hopton Wafers. P.42366. × 1·5.

FIG. 3. Uncrushed posterior region of dorsal disk with dorsal spine. Upton Cresset. P.41980. ×2.

FIG. 4. Part of dorsal disk with uncrushed right branchial and cornual plates. (*a*) Lateral view. Dairy Dingle. P.33795. × 1·5.

FIG. 5. Right cornual plate with part of dorsal disk. Dairy Dingle. P.29949. × 2.

FIG. 6. Part of dorsal disk with imperfect right branchial and cornual plates. Derrington Rea Bridge. P.34341. × 1·5.

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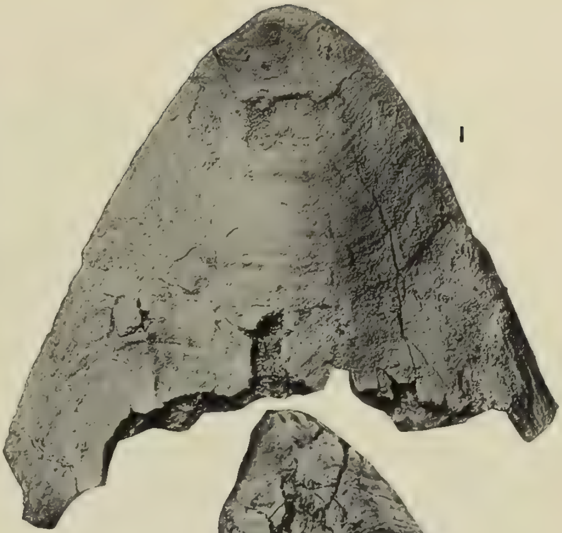

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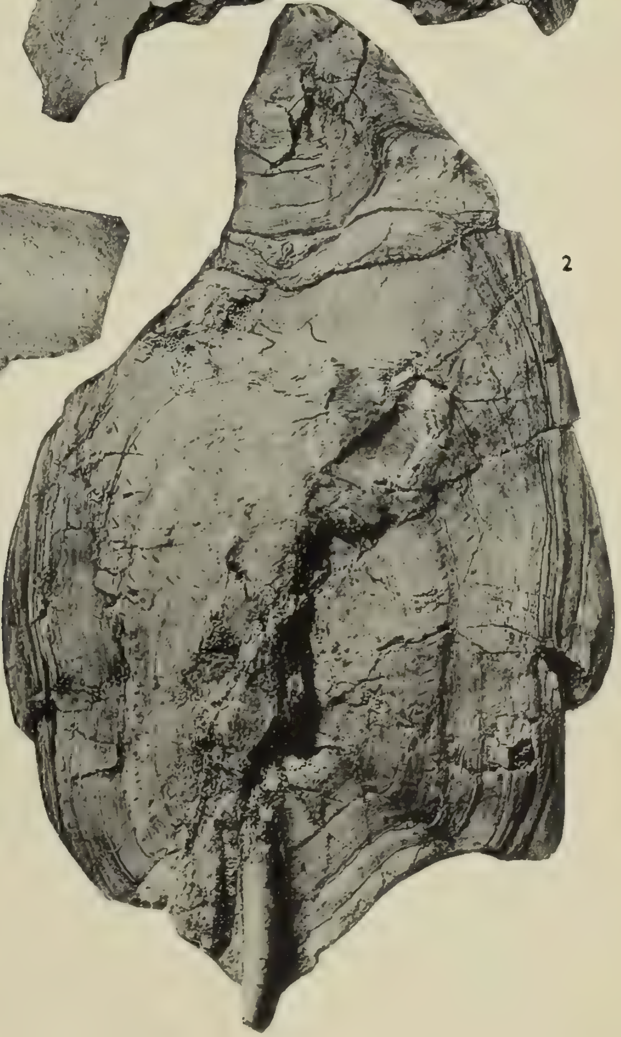

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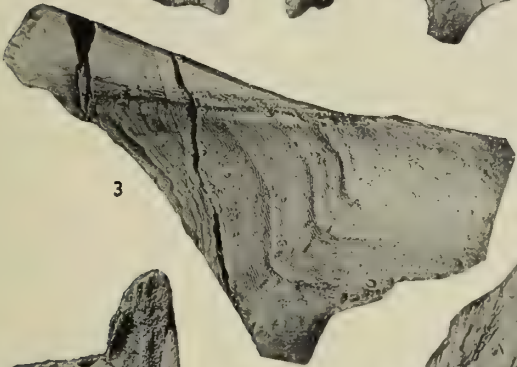

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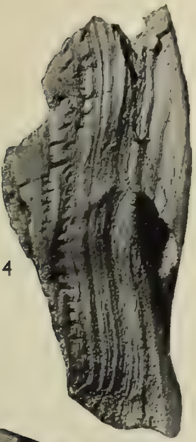

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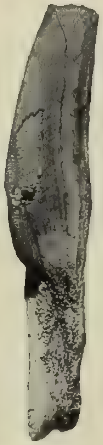

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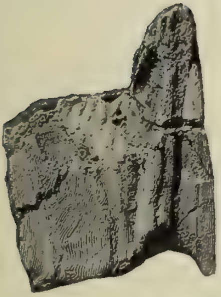

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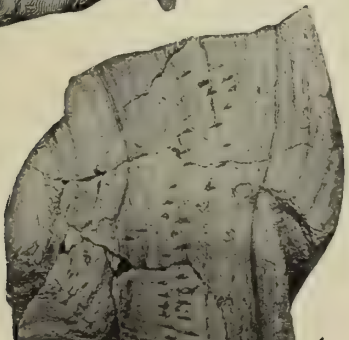


6

PTERASPIS

PLATE 34

Pteraspis (*Pteraspis*) *dairydinglensis* sp. nov.

FIG. 1. Rostral region. (*a*) Underside. Derrington Rea Bridge. P.32248. × 2.

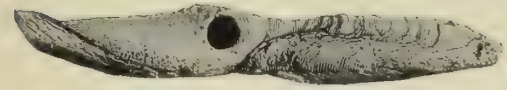
FIG. 2. Undersurface of rostral region. Derrington Rea Bridge. P.32249. × 2.

FIG. 3. Rostral region. Hopton Brook 4, Hopton Wafers. P.42361. × 2.

FIG. 4. Right orbital. Derrington Rea Bridge. P.32245. × 2.

Pteraspis (*Pteraspis*) *rostrata* var. *trimpleyensis* White

FIG. 5. Undersurface of rostrum. Guildings Brook, Worcestershire. P.16477. × 2.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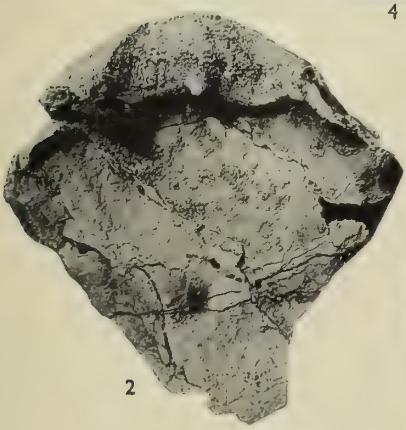
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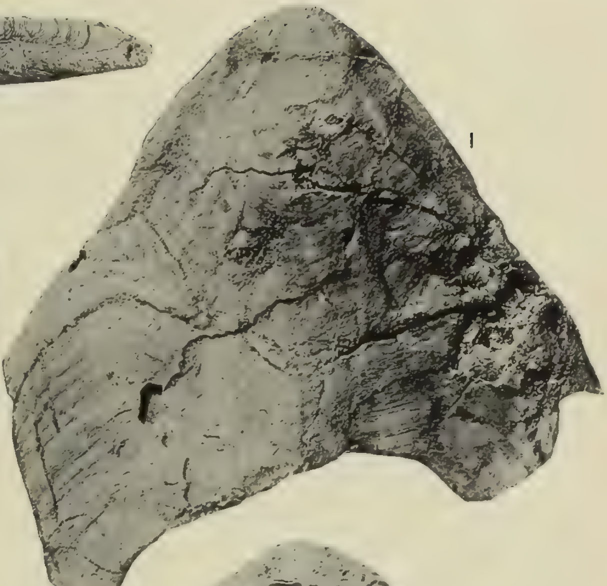
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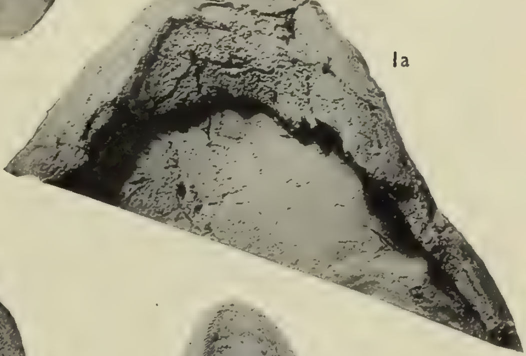
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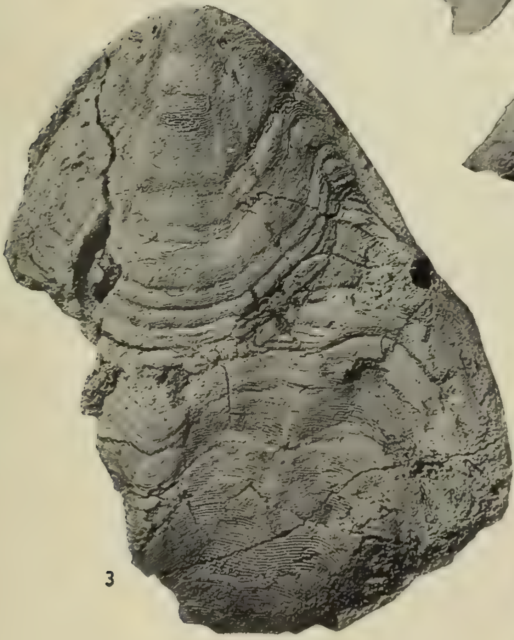
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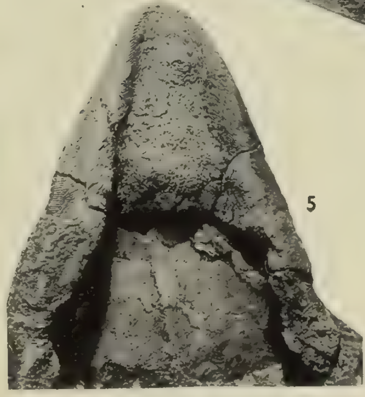
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PTERASPIS

PLATE 35

Pteraspis (*Pteraspis*) *rostrata* var. *trimpleyensis* White

FIG. 1. Rostral region. Ledwyche Brook. P.33766. × 1·5.

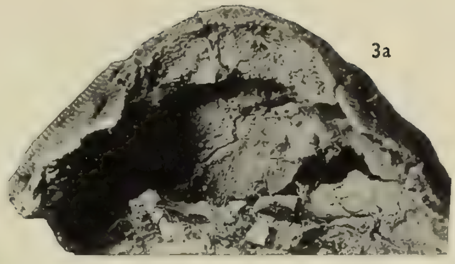
FIG. 2. Right half of small dorsal disk with dorsal spine. Oak Dingle. P.33573. × 1·5.

Pteraspis (*Simopteraspis*) *leathensis* White

FIG. 3. Imperfect dorsal shield. New Inn 1. P.34120. × 1·5. (*a*) Undersurface of rostrum.

Pteraspis (*Pteraspis*) *dairydinglensis* sp. nov.

FIGS. 4, 5. Ventral disks. Dairy Dingle. P.31901, P.29918. × 1·5.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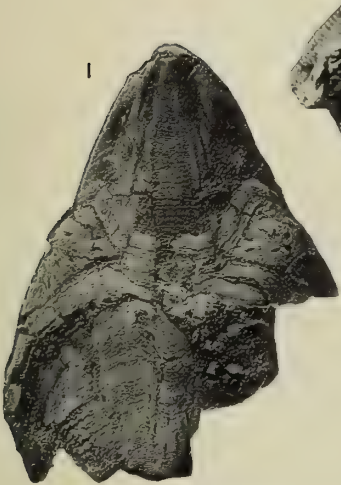
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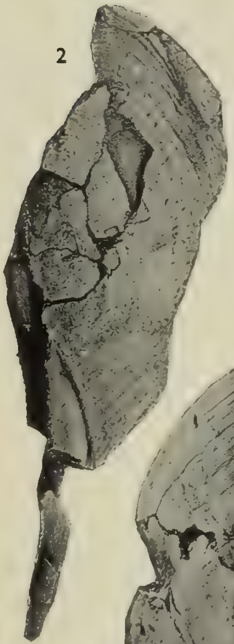
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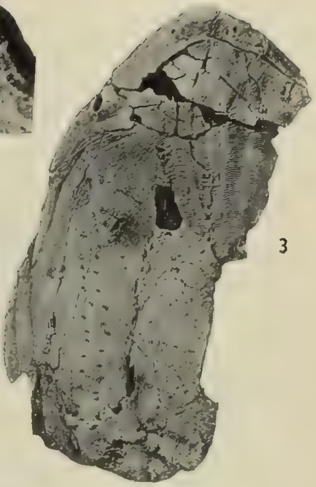
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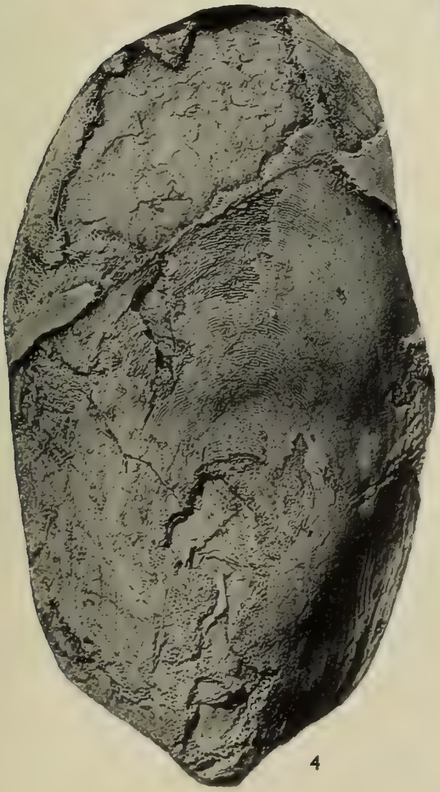
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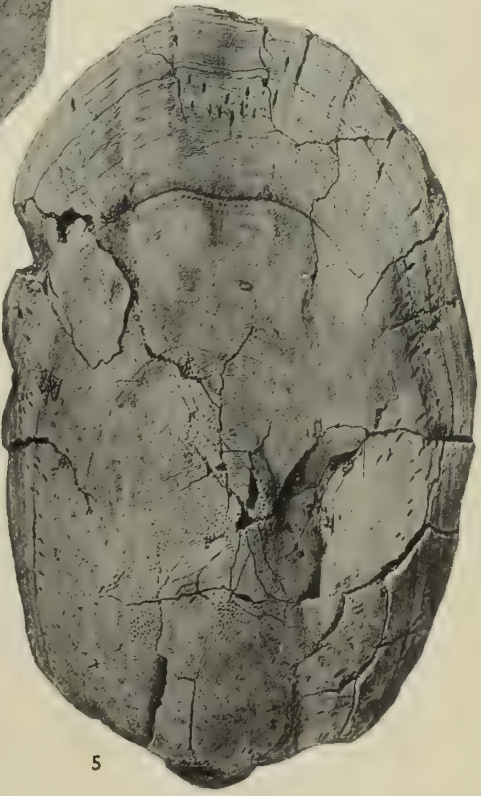
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PTERASPIS

PLATE 36

Cephalaspis bouldonensis sp. nov.

FIG. 1. Imperfect cephalic shield. The holotype. Bouldon Ford. P.43034. × 1·25.

Pteraspis (*Belgicaspis*) *crouchi* Lankester

FIG. 2. Branchial plate, anterior end missing. Heath Quarry, Bouldon. P.29853. × 2.

FIG. 3. Post-oral cover. Silvington, Waterfall. P.29844. × 4.

FIGS. 4, 5. Broad and narrow rostra from the same slab. Earnstrey Hall 1. P.27066. × 2.

FIGS. 6–8. Various shaped rostra, the first showing undersurface. Clee St. Margaret. P.32166, P.32164, P.32165. × 2.

FIGS. 9–11. Various shaped rostra. Silvington, Waterfall. P.29042. × 2; P.29830 × 2; P.29043. × 1·5.

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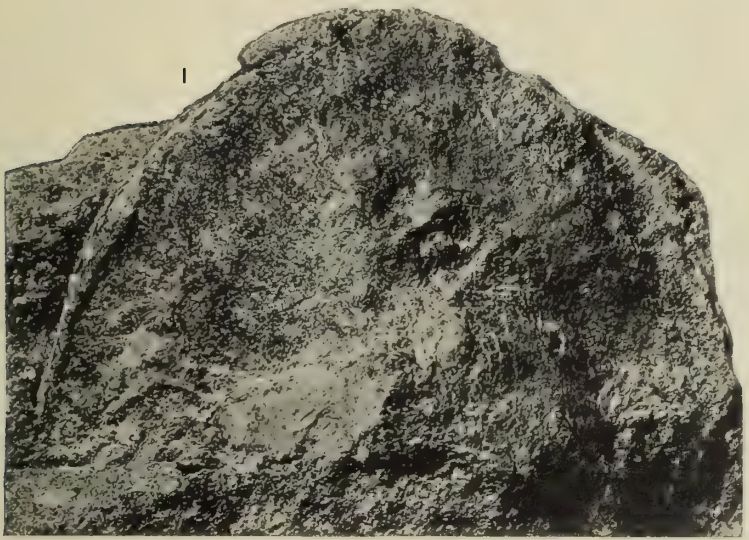

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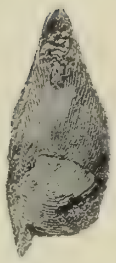

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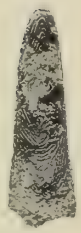

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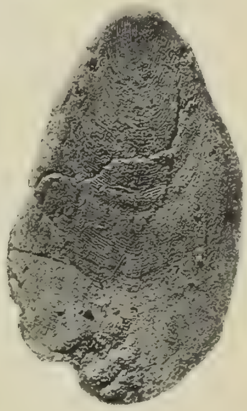

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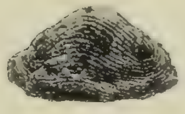

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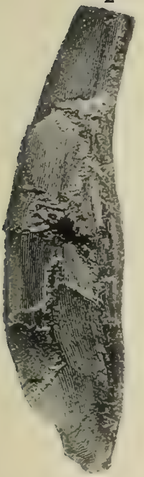

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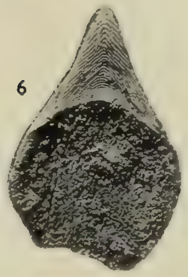

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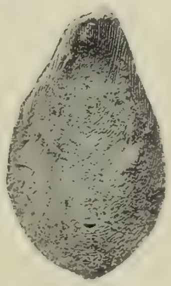

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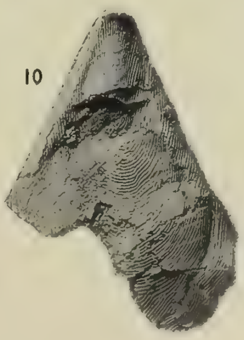

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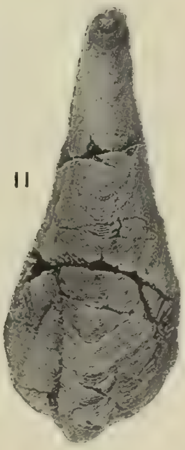

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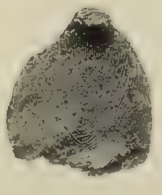


CEPHALASPIS & PTERASPIS

PLATE 37

Pteraspis (*Pteraspis*) *dairydinglensis* sp. nov.

Oral plates. Dairy Dingle. × 4.

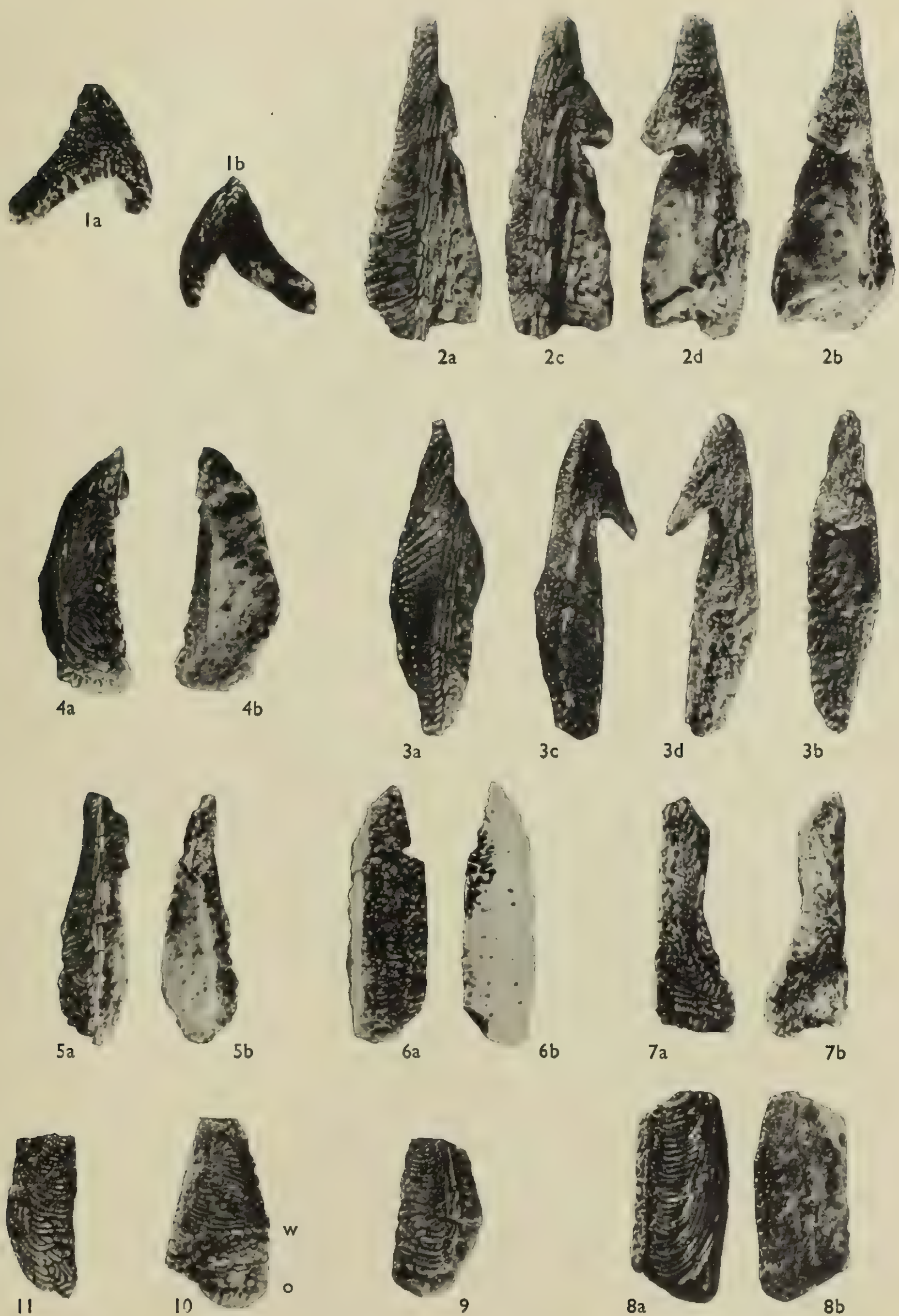
Fig. 1. Median plate. P.43709.

Figs. 2, 3. Near-median plates, Fig. 2 slightly imperfect basally. P.43710–11.

Figs. 4–7. Plates progressively more lateral in position. P.43712–15.

Figs. 8–11. Plates with heads broken away. Figs. 8, 11 are near-laterals with little or no overlapped areas ; Fig. 9, a left near-median plate with wide lateral and ventral overlapped areas ; Fig. 10 shows overlapped area at base only (*O*), and ornamented surface rubbed by movement against post-oral cover (*W*). P.43716–19.

a, *c*, aboral views ; *b*, *d*, oral views.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ORAL PLATES OF PTERASPIS

PLATE 38

Pteraspis (*Pteraspis*) *dairydinglensis* sp. nov.

FIGS. 1–3. Fixed lateral oral plates. P.43721–23.

FIGS. 4, 5. Anterior lateral plates. P.43730–31.

(*a*) outer ; (*b*) inner faces. All from Dairy Dingle. × 8.

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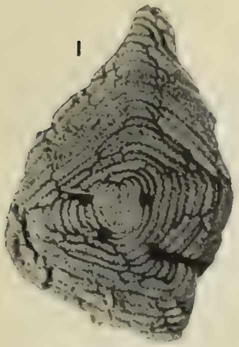

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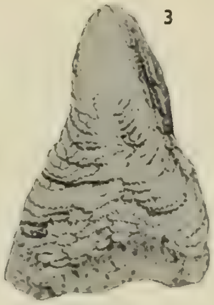

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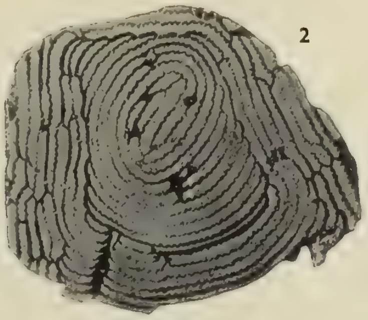

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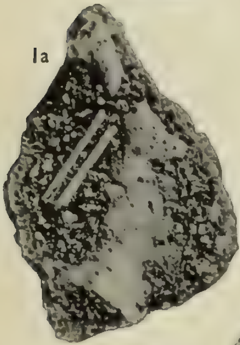

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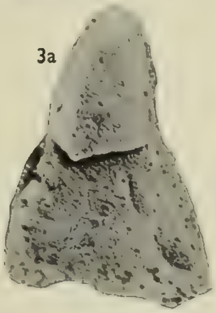

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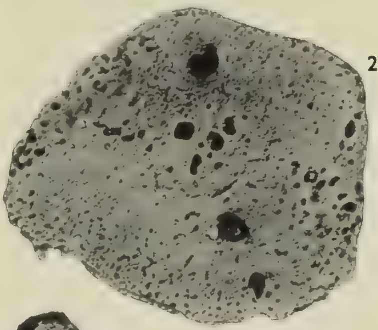

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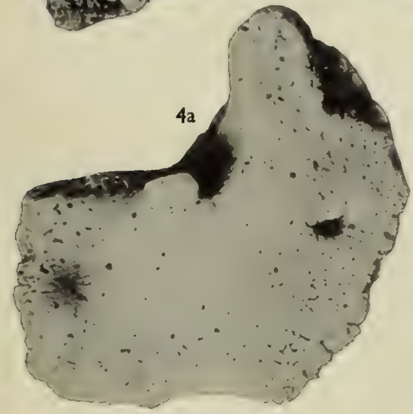

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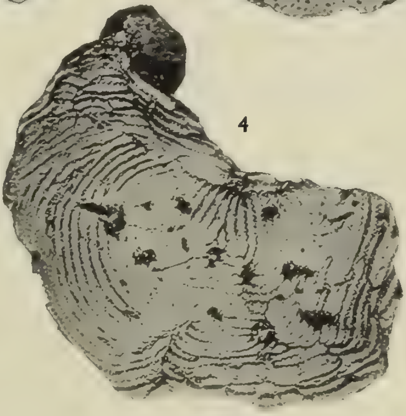

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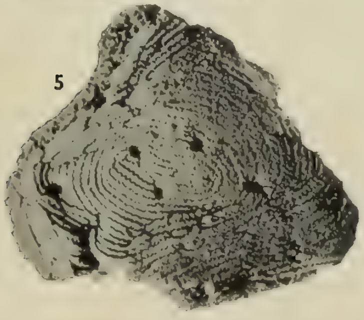

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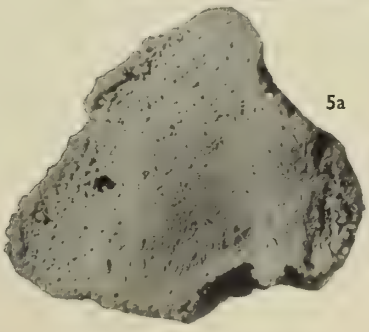


PTERASPIS

PLATE 39

Pteraspis (*Pteraspis*) *dairydinglensis* sp. nov.

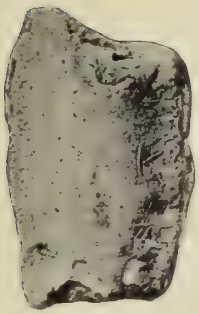
FIGS. 1–4. Posterior lateral plates. P.43700–03. × 6.

FIGS. 5–8. Post-oral covers. P.43704–07. × 6.

FIGS. 9–25. Lateral line scales. P.43601–17. × 4, except Fig. 14, × 8.

Figs. 11, 13, 15, 19, 20, 24, 25 show inner surfaces.

All from Dairy Dingle.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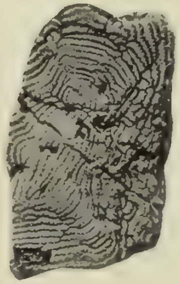
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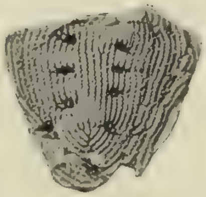
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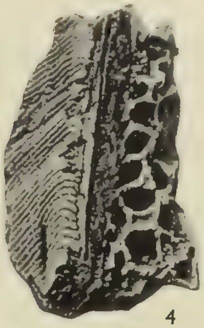
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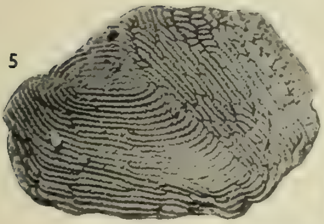
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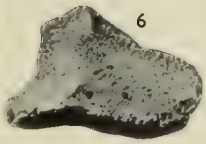
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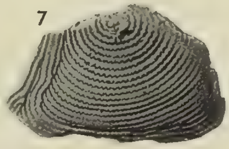
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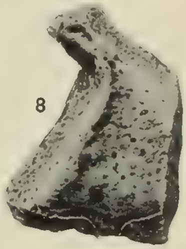
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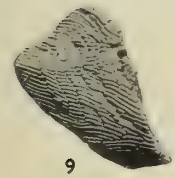
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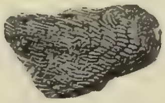
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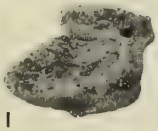
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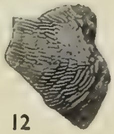
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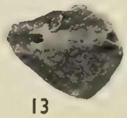
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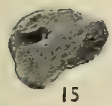
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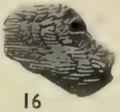
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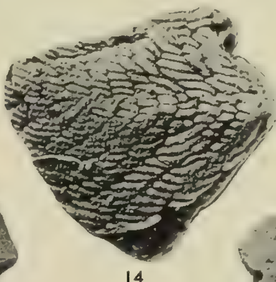
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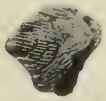
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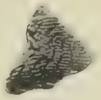
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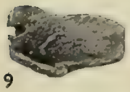
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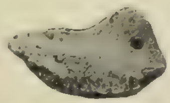
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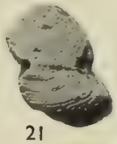
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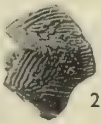
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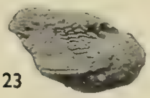
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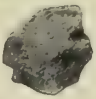
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PTERASPIS

PLATE 40

Pteraspis (*Pteraspis*) *dairydinglensis* sp. nov.

FIGS. 1–3. Dorsal ridge-scales. (Fig. 1, inner surface.) P.43618–20.

FIG. 4. Imperfect asymmetrical ridge-scale. P.43621.

FIGS. 5, 6. Imperfect ventral ridge-scales showing signs of wear. P.43622, P.43624.

FIGS. 7–9. Posterior ridge-scales. P.43625–27.

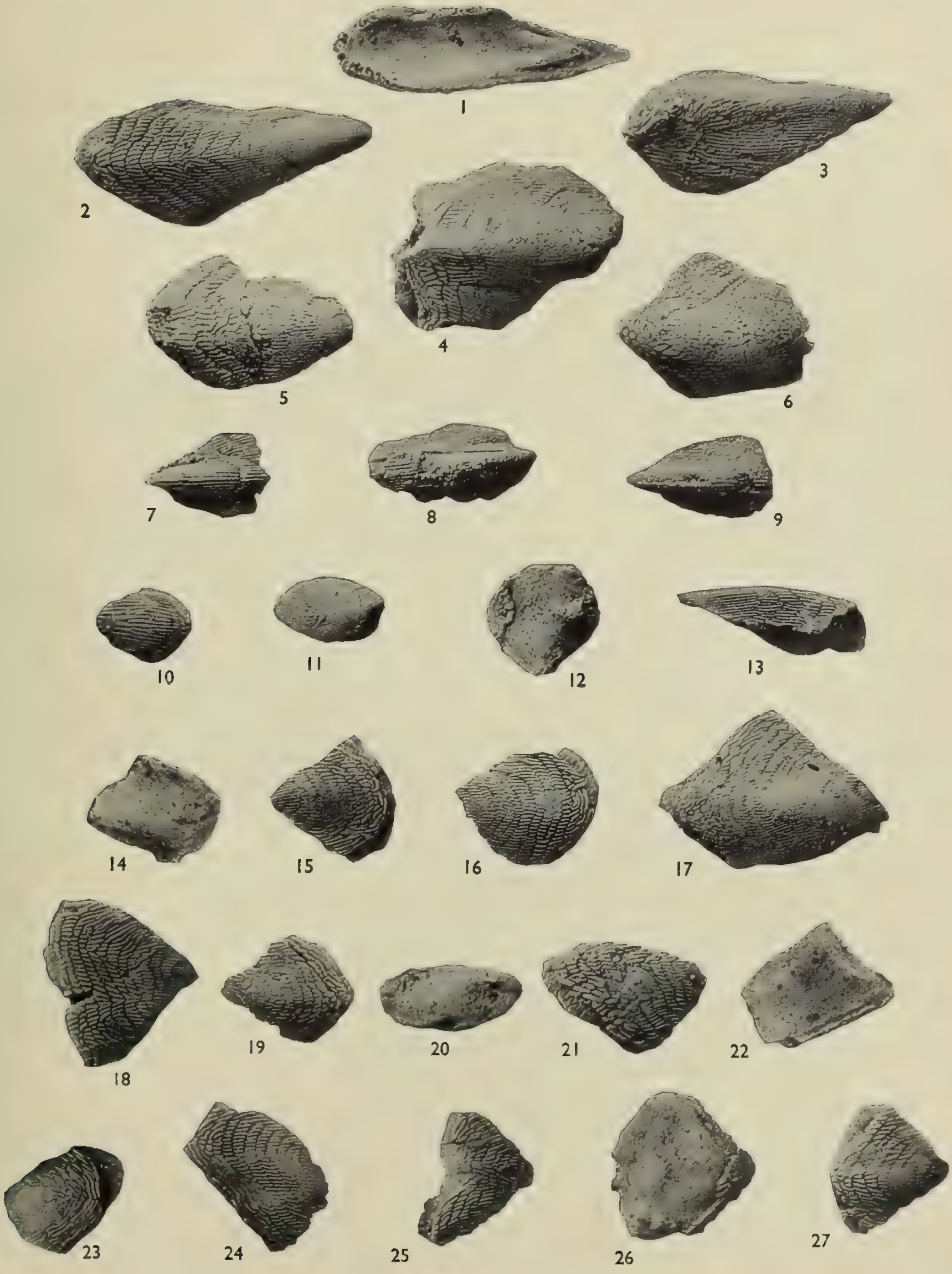
FIGS. 10, 11. Anterior ventral ridge-scales. P.43629–30.

FIG. 12. Anterior ventral ridge-scale showing ornament on undersurface. P.43631.

FIG. 13. Anterior ridge-scale of tail. P.43632.

FIGS. 14–27. Flank-scales. Figs. 14, 20, 22, 26 show undersurfaces, the last two with ornamentation. P.43633–37, P.43668–69, P.43639–40, P.43671, P.43643–46.

All from Dairy Dingle. × 4.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PTERASPIS

PLATE 41

Pteraspis (Pterapis) dairydinglensis sp. nov.

FIGS. 1–22, 24. Flank-scales. Figs. 2, 17 show undersurfaces. Dairy Dingle. P.43641–42, P.43647–56, P.43658, P.43660, P.43667, P.43676, P.43678, P.43682–83, P.43686, P.43689, P.43693, P.43692.

FIGS. 23, 25–27. Caudal scales. Fig. 27 shows the undersurface. Dairy Dingle. P.43690, P.43695, P.43694, P.43696.

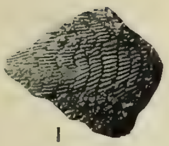
FIG. 28. Irregular scale of unknown position. Dairy Dingle. P.43698.

FIGS. 29–31. Flank-scales. Derrington Rea Bridge. P.44395, P.44398, P.44396.

FIGS. 32–37. Various ridge-scales. Upton Cresset. P.42873, P.42872, P.42874, P.42877, P.42876, P.42881.

FIGS. 38–44. Various flank-scales. Upton Cresset. P.42897, P.42893, P.42894, P.42901, P.42900, P.42904, P.42884.

All × 4.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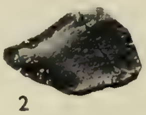
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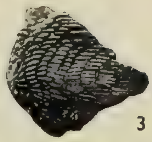
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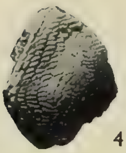
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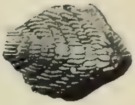
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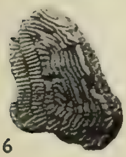
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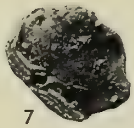
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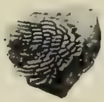
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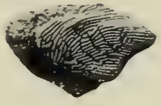
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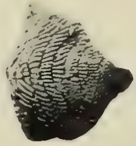
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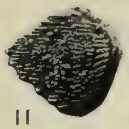
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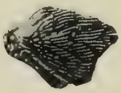
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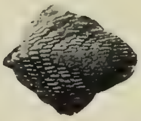
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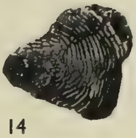
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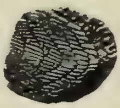
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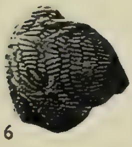
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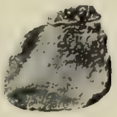
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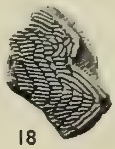
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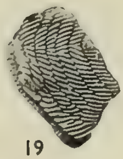
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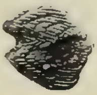
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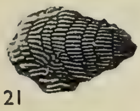
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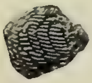
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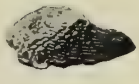
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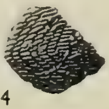
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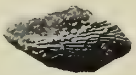
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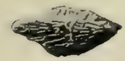
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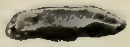
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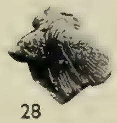
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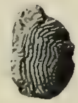
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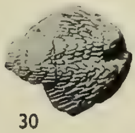
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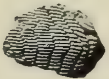
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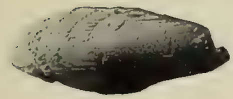
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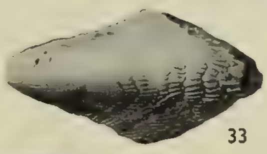
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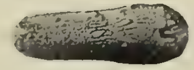
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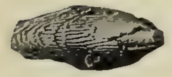
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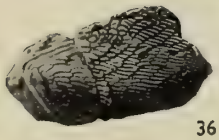
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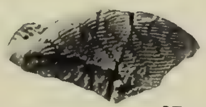
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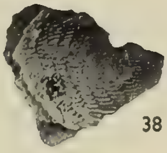
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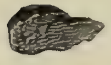
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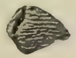
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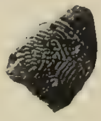
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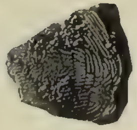
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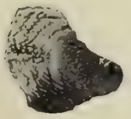
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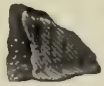
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PTERASPIS

PLATE 42

Ischnacanthus wickhami sp. nov.

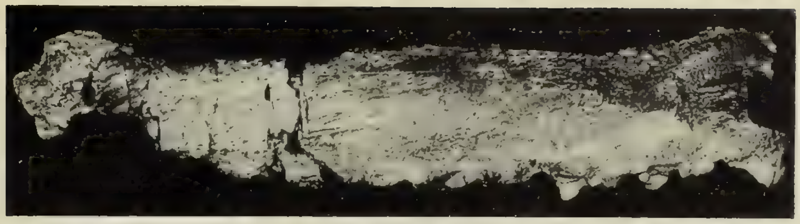
FIG. 1. Part of upper jaw with worn dentition. Man Brook 4, Trimpley, Worcestershire. P.17451. × 1·5.

FIG. 2. Part of upper jaw. *a*, Oral view. Gardener's Bank, Cleobury Mortimer. The holotype. P.24625. × 1·5.

FIG. 3. Part of upper margin of lower jaw. *a*, Oral view. Hudwick Dingle 1. P.29725. × 2·5.

Ischnacanthus kingi sp. nov.

FIG. 4. Right lower jaw. Baggeridge Colliery, South Staffordshire. P.15362. × 1·5.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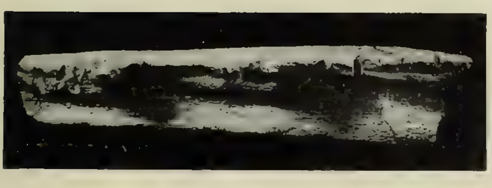
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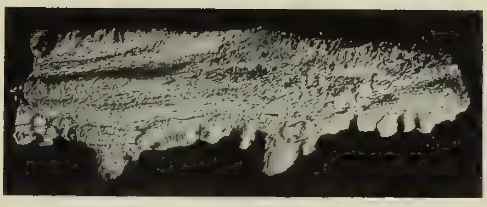
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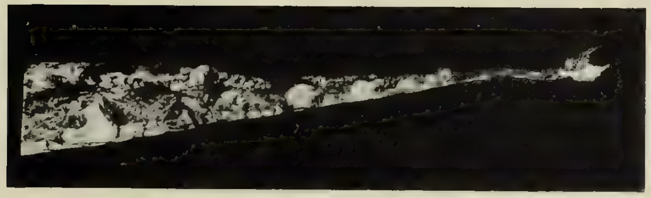
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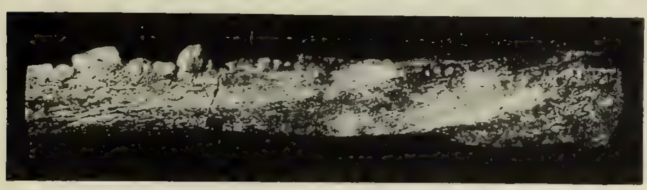
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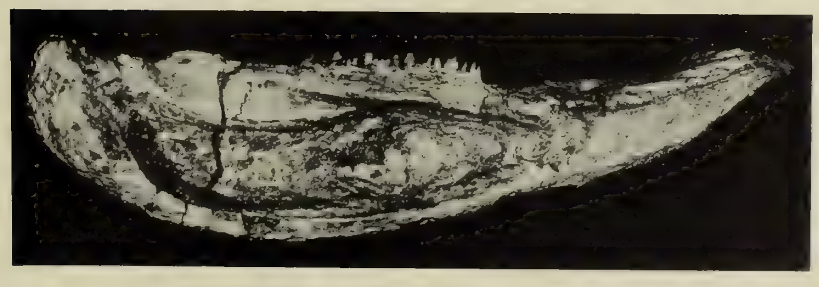
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ISCHNACANTHUS

PLATE 43

Protaspis (*Europrotaspis*) *crenulata* sp. nov.

FIG. 1. Imperfect dorsal disk. Upper Overton Quarry. P.29415. × 2.

FIG. 2. Posterior end of left branchial plate with part of dorsal disk attached. Part of holotype. Besom Farm Quarry. P.28801. × 2.

FIG. 3. Part of holotype showing specimens of *Spirobis* sp. which were attached to inner surface of dorsal disk. Besom Farm Quarry. P.28801. × 7.

FIG. 4. Impression of part of dorsal disk showing discontinuous ornamentation. Besom Farm Quarry. P.28879. × 3.

FIG. 5. Flank-scale. Besom Farm Quarry. P.29068. × 8.

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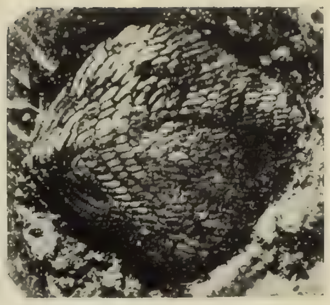

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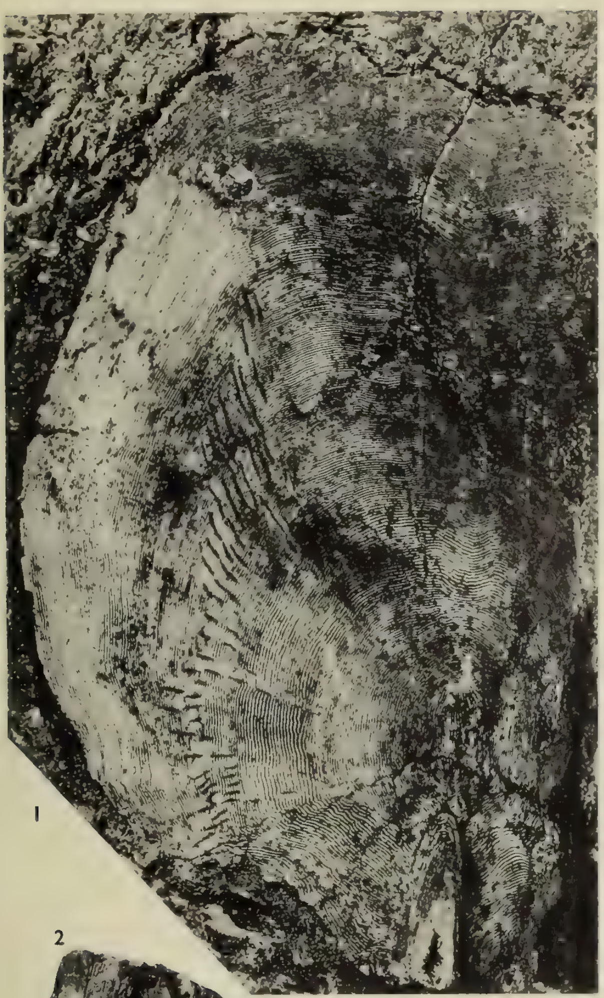

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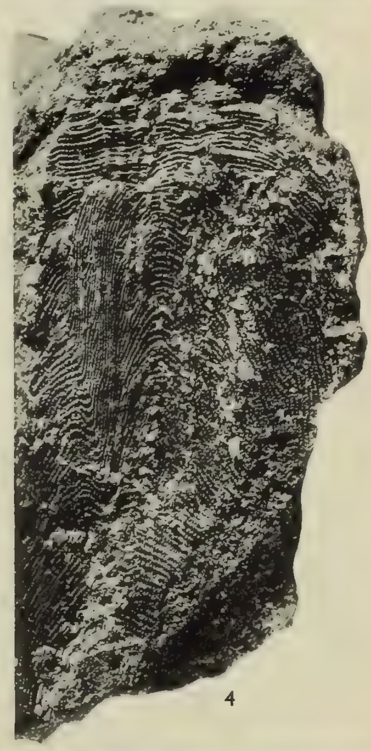

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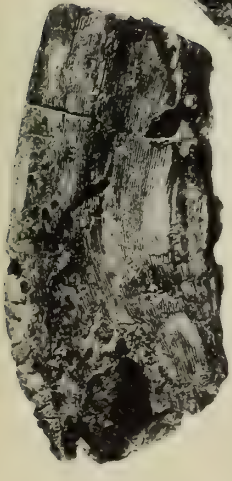

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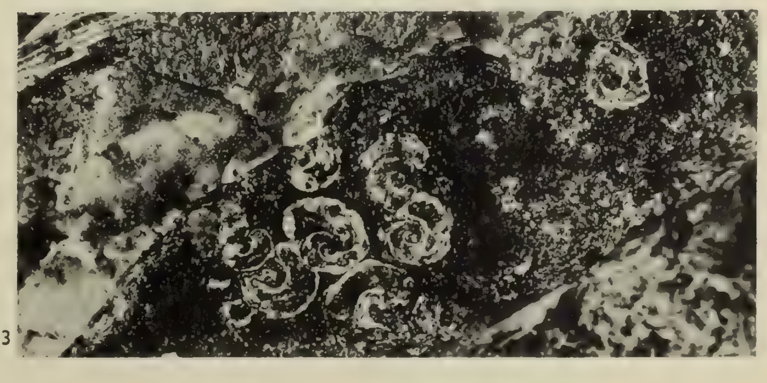


PROTASPIS

PLATE 44

Protaspis (*Europrotaspis*) *crenulata* sp. nov.

FIG. 1. Imperfect ventral disk, largely in impression. Besom Farm Quarry. P.26311. × 1·5.

FIG. 2. Dorsal (?) ridge-scale. Newton Dingle 2, Loughton. P.29386. × 7.

FIG. 3. (?) Ventro-lateral ridge-scale. Besom Farm Quarry. P.29077. × 8.

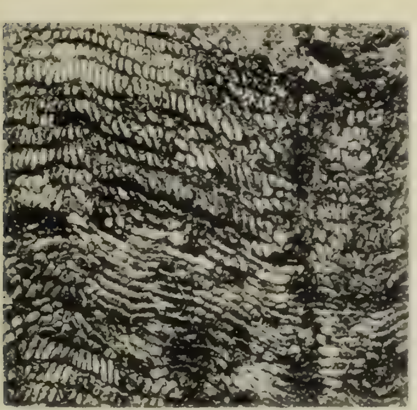
FIG. 4. Part of Fig. 3 further enlarged to show details of ornamentation. × 20.

FIG. 5. Slightly worn ornamentation on dorsal disk. Upper Overton Quarry. P.31642. × 20.

FIG. 7. Part of left anterior border of ventral disk showing irregularity of ornamentation. Besom Farm Quarry. P.29479. × 5.

Protaspis (*Europrotaspis*) *arnelli* Brotzen

FIG. 6. Ornament of dorsal disk. Stage IIIb. Kujdanow, Podolia. (N.H.M. Stockholm P.106.) × 20.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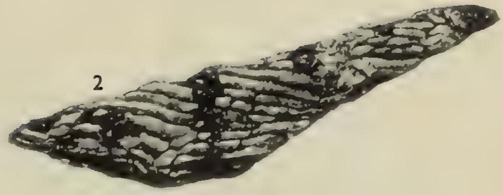
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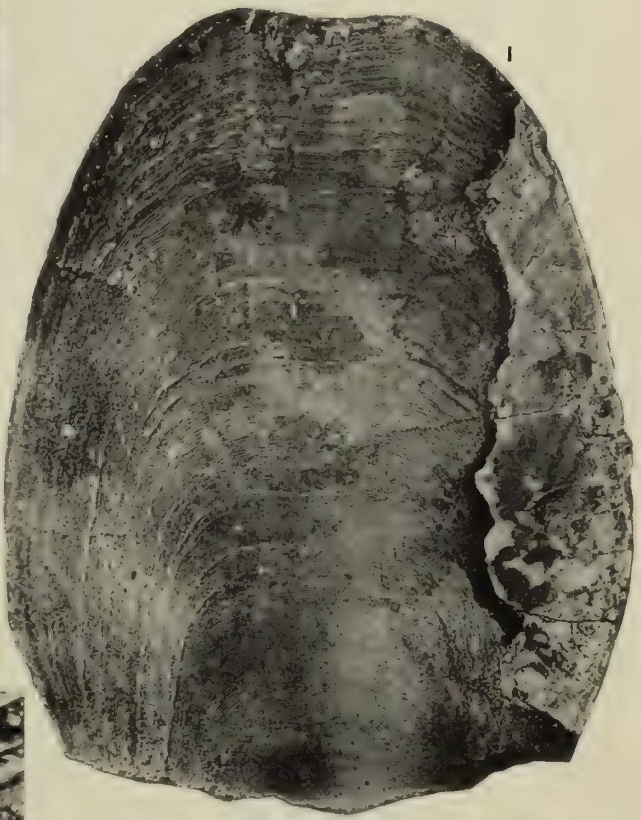
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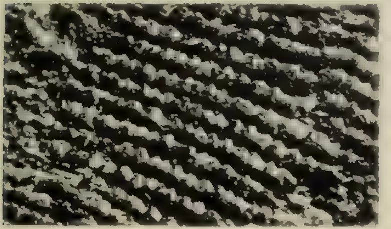
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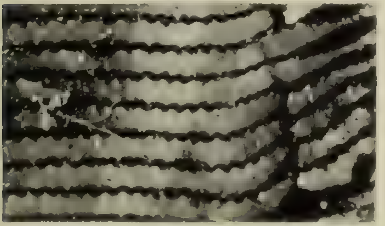
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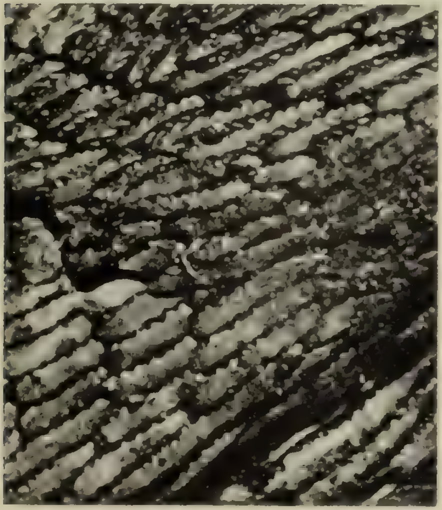
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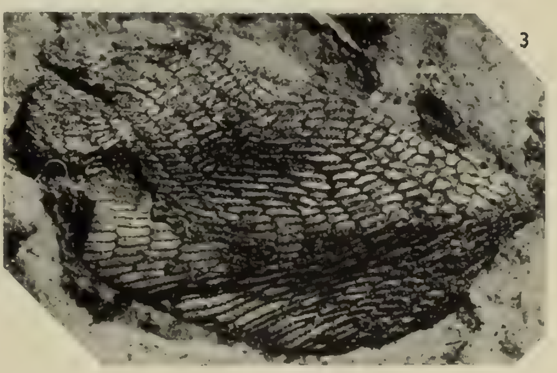

3

PROTASPIS

PLATE 45

FIG. 1. *Pteraspis* (*Cymripteraspis*) *leachi* White. Flank-scale. Swanlake Bay, Pembrokeshire. P.29329. × 8.

FIG. 2. *Pteraspis* (*Cymripteraspis*) *leachi* White. Flank-scale. Prescott Reaside. P.29261. × 8.

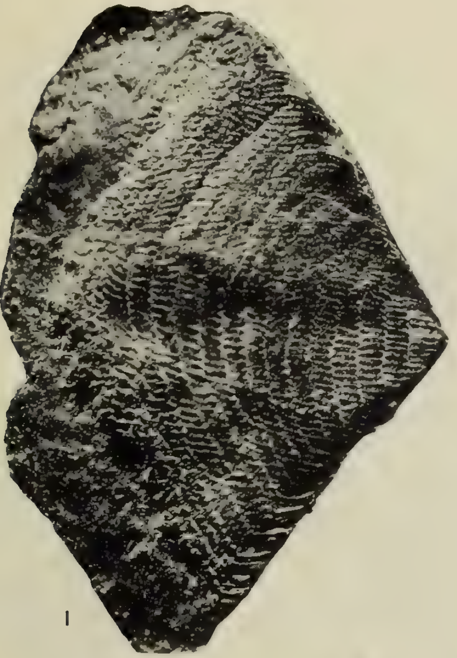
FIG. 3. Tooth of Acanthodian. Besom Farm Quarry. P.28903. × 5.

FIG. 4. *Ischnacanthus* (?) *anglicus* sp. nov. Median fin-spine with restored dorsal view. (*a*) Right side view. The holotype. Besom Farm Quarry. P.29082. × 3.

FIG. 5. *Onchus wheathillensis* sp. nov. Median fin-spine. The holotype. Besom Farm Quarry. P.29083. × 3.

FIG. 6. *Overtonaspis billballi* gen. et sp. nov. Right anterior lateral plate. The holotype. Upper Overton Quarry. P.29272. × 1·5.

FIG. 7. *Kujdanowiaspis anglica* (Traquair). Imperfect right anterior ventro-lateral plate. New House Farm, Neenton. P.29821. × 1·5.



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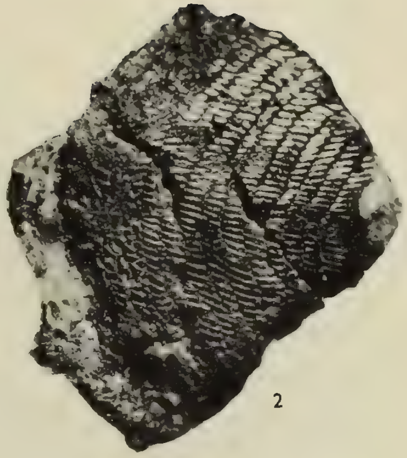

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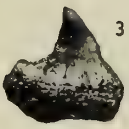

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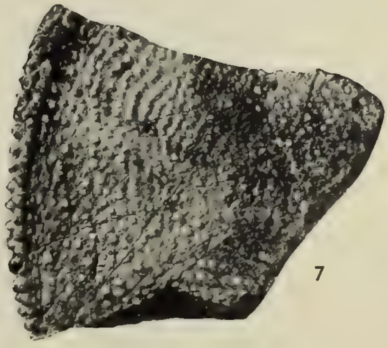

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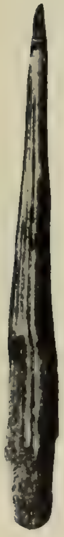

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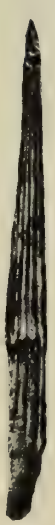

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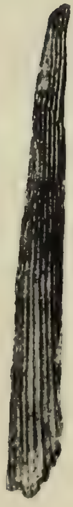

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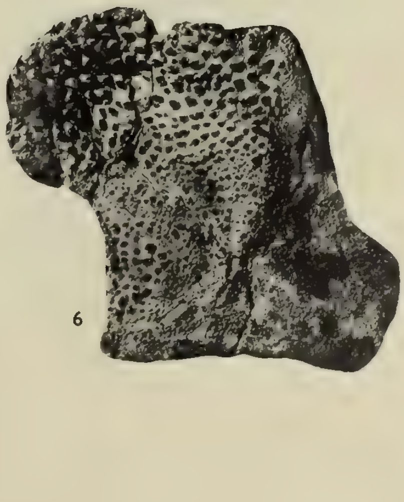

6

PTERASPIS, ACANTHODIANS and ARTHRODIRES

PLATE 46

Fig. 1. *Kujdanowiaspis willsi* sp. nov. Left spinal plate, dorsal view. The holotype. Besom Farm Quarry. P.28913. × 5.

Fig. 2. *Kujdanowiaspis willsi* sp. nov. Left central plate, referred to this species. Besom Farm Quarry. P.28889. × 3.

Fig. 3. *Prescottaspis dineleyi* gen. et sp. nov. Median scute. Prescott Reaside. P.29267. × 7.

Fig. 4. *? Prescottaspis dineleyi* gen. et sp. nov. Left posterior ventro-lateral plate without surface ornamentation, possibly of this species. Prescott Reaside. P.29259. × 3.

Fig. 5. *Wheathillaspis wickhamkingi* gen. et sp. nov. Imperfect anterior ventro-lateral and spinal plates. The holotype. Besom Farm Quarry. P.28908. × 4.

Fig. 6. Lateral scale of an arctolepid. Upper Overton Quarry. P.29756. × 3.

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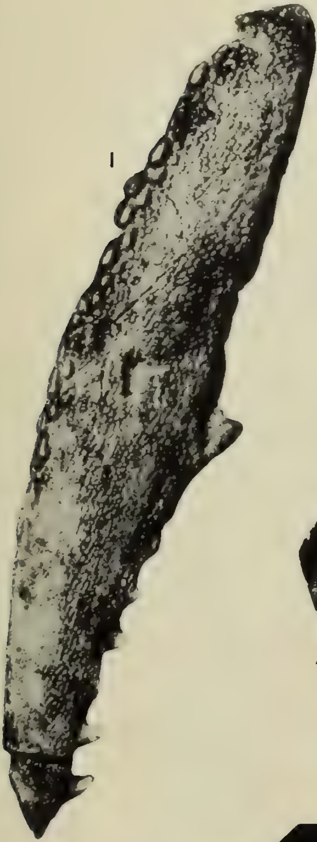

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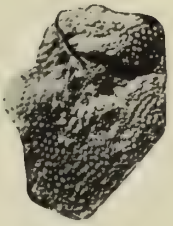

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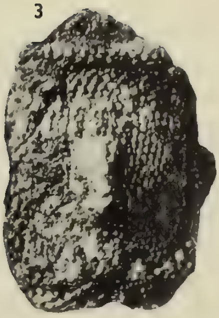

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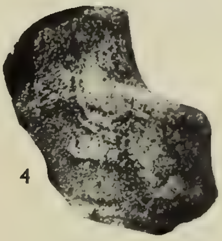

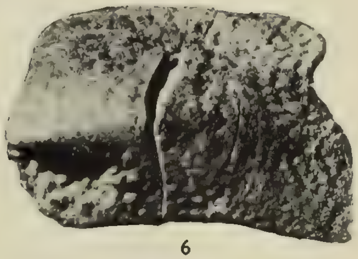

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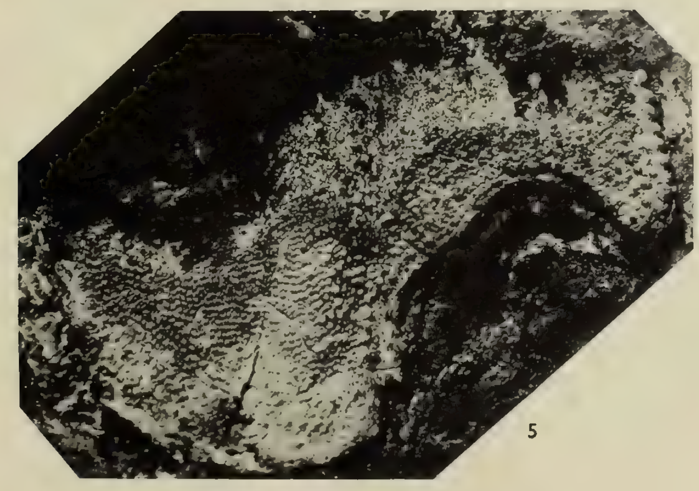


5

ARTHRODIRES

PLATE 47

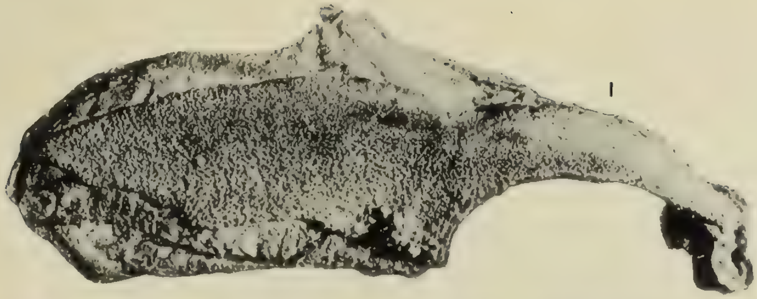
Pseudosauripterus anglicus (A. S. Woodward)

FIG. 1. Cast of right entopterygoid, oral view. Church Quarry, Farlow. P.27176. × 1·5.

FIGS. 2–4. External impressions of scales of paratype block, with light reversed to give positive effect. Church Quarry, Farlow. P.200*a*. × 2.

FIG. 5. External impressions of scales on counterpart of type-block, with lighting reversed. Scale on right is the underside of that figured by A. S. Woodward, 1891, pl. 16, fig. 6. Church Quarry, Farlow. P.7601. × 2.

1



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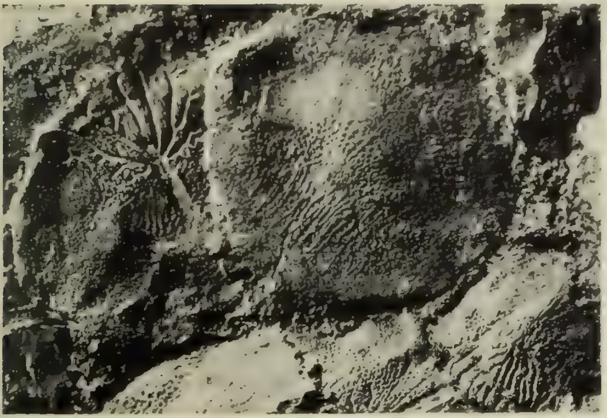

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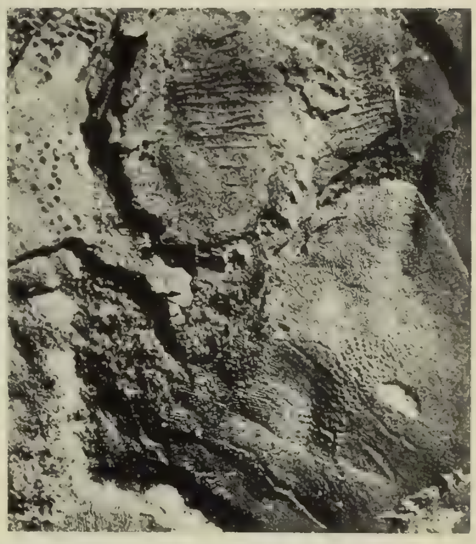

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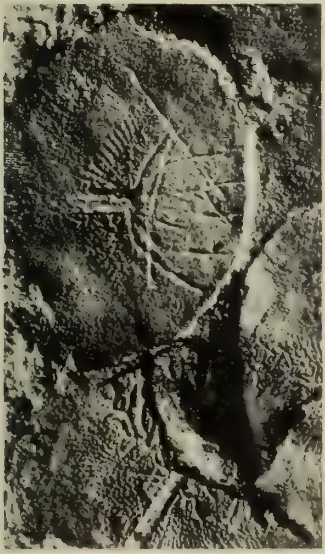

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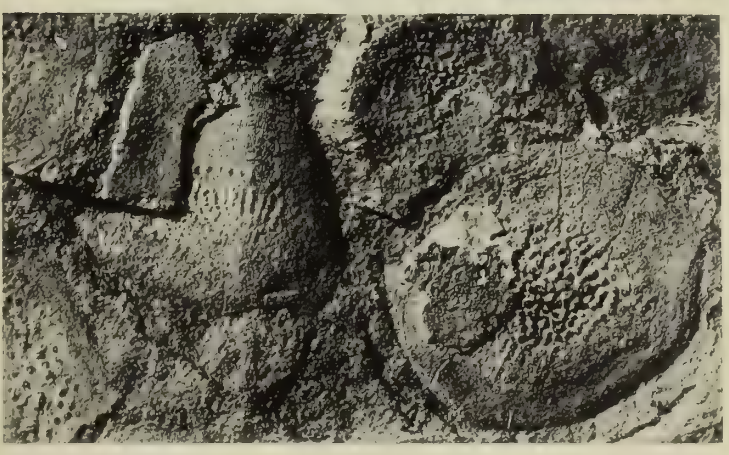


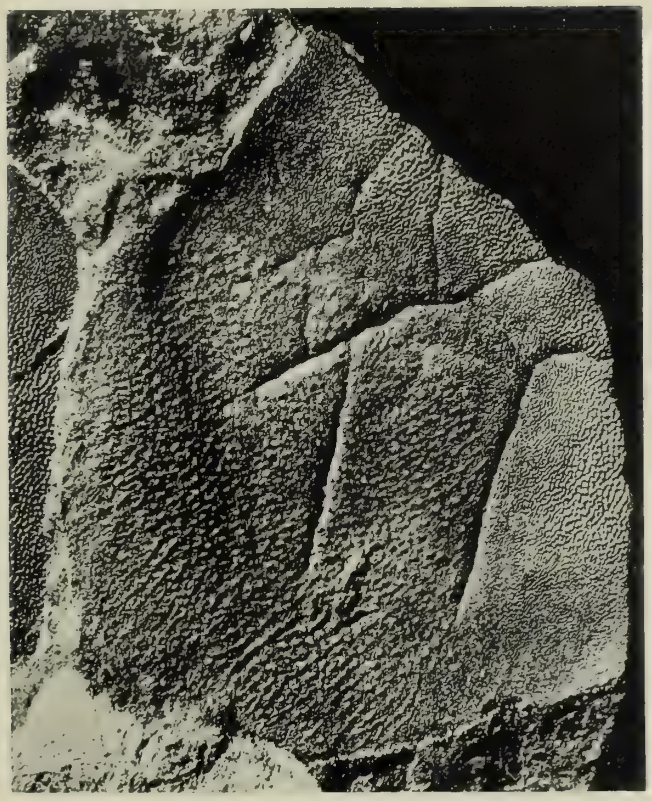
PSEUDOSAURIPTERUS

PLATE 48

Sauripteris taylori Hall

Fig. 1. External impression of scale with lighting reversed to give positive effect. The cracks are of *post-mortem* origin. Blossburg Red Beds, Cassadaga Stage, lower Upper Devonian, near Blossburg, Tioga County, Pennsylvania. P.43518. × 2.

Figs. 2, 3. Scales from same slab as Fig. 1. Nat. size.



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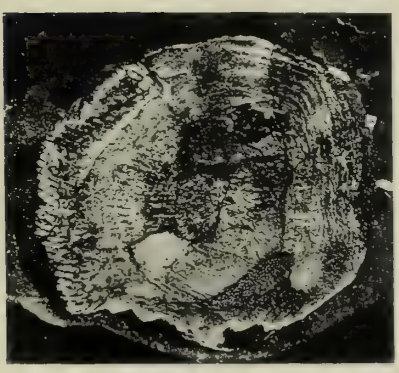

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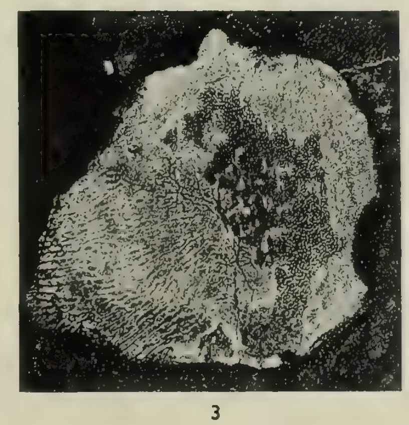

3

SAURIPTERIS

THE ORDOVICIAN TRILOBITE FAUNAS OF SOUTH SHROPSHIRE, II

W. T. DEAN

BRITISH MUSEUM
30 NOV 1961
NATURAL HISTORY

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 5 No. 8
LONDON: 1961

THE ORDOVICIAN TRILOBITE FAUNAS OF SOUTH SHROPSHIRE, II

BY

WILLIAM THORNTON DEAN

Pp. 311–358 ; *Pls.* 49–55

BRITISH MUSEUM
10 NOV 1961
NATURAL HISTORY

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 5 No. 8
LONDON: 1961

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THE ORDOVICIAN TRILOBITE FAUNAS OF SOUTH SHROPSHIRE, II

By WILLIAM THORNTON DEAN

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SYNOPSIS

The present paper is the second of four describing and figuring the trilobites of the Caradoc Series in south Shropshire. The families dealt with include the proparian Cheiruridae, Encrinuridae, Dalmanitidae and Pterygometopidae, and the gonatoparian Homalonotidae. These comprise nine genera and subgenera, containing seventeen species and subspecies, five of them new. The type-species of *Phacopidina* Bancroft is redescribed, the genus being removed from the subfamily Calmoniinae and assigned to the subfamily Acastinae as a subgenus of *Kloucekia* Delo.

SYSTEMATIC DESCRIPTIONS

Family CHEIRURIDAE Salter, 1864

Subfamily ACANTHOPARYPHINAE Whittington & Evitt, 1953

Genus *ACANTHOPARYPHA* Whittington & Evitt, 1953

TYPE SPECIES. *Acanthoparypha perforata* by original designation of Whittington & Evitt (1953 : 72).

Acanthoparypha stubblefieldi (Bancroft)

(Pl. 49, figs. 1, 3–6, 11)

1949. *Nieszkowskia stubblefieldi* Bancroft, p. 311, pl. 10, figs. 26, 27.
1958. *Nieszkowskia stubblefieldi* Bancroft : Dean, pp. 201, 219.

The only figure of the cranidium of the species published by Bancroft (1949, pl. 10, fig. 26) shows an incomplete and somewhat distorted internal mould which has apparently been slightly compressed laterally and sheared dextrally. It is necessary, therefore, to redescribe the species and to figure topotype material showing the true glabellar form. Bancroft's photograph does not give a true impression of the proportions of the glabella, and also exaggerates the angle at which the glabellar furrows are directed backwards.

DESCRIPTION. In plan the glabellar outline is subrectangular, with the frontal lobe only slightly convex forwards and the anterolateral margins and angles becoming respectively slightly convergent and rounded. The glabella is moderately convex both longitudinally and transversely, its length being estimated as slightly greater than the maximum breadth, measured across the second and third glabellar lobes. The anterior border is imperfectly preserved, but appears to be small and narrow (*sag.*). There are three pairs of glabellar lobes, those of the third pair being slightly the largest. The frontal glabellar lobe is short (*sag.*), less than one-fifth of the length of the glabella, and broad ; frontally it is almost transversely straight, but the anterolateral margins are broadly rounded. The first glabellar furrows are deep, shallowing adaxially and curving inwards and backwards from the axial furrows for almost one-third the breadth of the glabella. The first glabellar lobes are subrectangular in plan and of uniform length (*exsag.*). The second glabellar furrows are deep, parallel to the first pair of furrows but turning slightly backwards at their proximal ends ; in one specimen (Pl. 49, figs. 1, 4) the right-hand furrow of the second pair does not quite attain the axial furrow, but there is insufficient material to ascertain whether this is an exceptional case. The second glabellar lobes are of similar shape to those of the first pair, and of only slightly smaller size. The third glabellar furrows are deep, more or less parallel to the other pairs of furrows. They extend inwards from the axial furrows at an angle of about 65–70 degrees, but towards their proximal ends they turn back sharply through about 30 degrees and extend towards, though they do not reach, the occipital furrow. The proximal ends of the three pairs of glabellar furrows are almost longitudinally in line, forming a median body of uniform breadth.

The third glabellar lobes are larger than the other pairs and tend towards the so-called " cat's ear " outline (see Pl. 49, fig. 6), whilst the gently convex posterior margins give a sinuous appearance to the moderately deep occipital furrow. The occipital ring curves forwards slightly towards the axial furrows and is broader (*sag.*) than the posterior border ; only the proximal parts of the latter are known and they are transversely straight. The fixigenae, librigenae and facial sutures have not been found preserved.

The hypostoma and thorax are unknown.

Only one specimen of the pygidium is available and, although incomplete, is estimated to have been slightly wider than long. The axis is roughly triangular with three axial rings and occupies one-third of the frontal breadth of the pygidium. First axial ring is narrow (*sag.*), curved sharply backwards distally where there are poorly-defined axial furrows. Beyond the axial furrows the pleurae of the first pair become suddenly and markedly wider (*exsag.*) and are produced posteriorly as a pair of large spines. The anterior edge of each pleura runs transversely straight from the axial furrow and then turns sharply backwards through a right angle to form the lateral margin of the pygidium. The posterior edges of the same pleurae almost coalesce with the second pleurae, being separated from them by only shallow interpleural furrows which extend posteriorly, parallel to the lateral margin until just beyond the tip of the axis ; they then diverge backwards markedly and finally intersect the lateral margins so as to form long, stout pleural spines. The second pleurae are nearly continuous with the second axial ring, beyond the distal ends of which they are directed almost straight backwards as a pair of large, parallel spines, the bases of which meet proximally. Between their point of contact and the second axial ring is situated the third axial ring. This is not differentiated from its corresponding pleurae which converge sharply backwards and inwards, and meet to form a sub-triangular area with a central depression.

The surface of the glabella is covered with large tubercles, interspersed with smaller granules. Similar, though more closely crowded tubercles ornament the axial rings of the pygidium, whilst on the side-lobes they are much more dispersed. All the furrows on both cranidium and pygidium are smooth.

HORIZON AND LOCALITY. *Acanthoparypha stubblefieldi* is known as yet from only one locality in south Shropshire, the old cartway section near the south-eastern corner of Smeathen Wood, Horderley, 250 yards west-south-west of Wood House. The horizon is in the Smeathen Wood Beds, Harnagian Stage, zone of *Reuscholithus reuschi*.

LECTOTYPE, here selected. BM. In. 42084*a*, *b* (Pl. 49, figs. 5, 11).

PARATYPE. BM. In. 52085 (Pl. 49, fig. 3).

FIGURED SPECIMENS. BM. In. 50498 (Pl. 49, fig. 1); BM. In. 50499 (Pl. 49, fig. 6).

DISCUSSION. The genus *Acanthoparypha*, although close to *Nieszkowskia* Schmidt, was separated by Whittington & Evitt so as to include only those *Nieszkowskia*-like forms which lack the glabellar spine such as is found in *N. cephaloceros* (Nieszkowski) the type species. They were unable to differentiate between the two genera on the basis of the pygidia.

Acanthoparypha perforata (Whittington & Evitt, 1953 : 73, pl. 13, figs. 2, 4–6 ; pls.

14–16; pl. 17, figs. 1–6), from the Edinburg Limestone of Virginia, is easily distinguished from *A. stubblefieldi* by its strongly convex glabella, the sides of which are more convergent anteriorly, and by the proportionately longer pygidium, with four long, subequal spines and only one fully-developed ring furrow, behind which is situated a deep, mesial pit.

The cephalon of *Acanthoparypha chiropyga* (Whittington & Evitt, 1953 : 77, pl. 28, figs. 31–44; pl. 29; pl. 30, figs. 1–28, from the Lincolnshire Limestone of Virginia, possesses less coarsely-developed tuberculation than that of *A. perforata*. In this respect, and also in having better-defined glabellar furrows, it approaches *A. stubblefieldi* but can be separated from the latter by means of its more tapered glabellar outline and by its pygidium, only the first axial ring of which is known, but which has four pleural projections of almost equal size, and carries several large tubercles on its upper surface. Both these North American species are lower Middle Ordovician in age, and occur respectively at horizons which are generally contemporaneous with, and slightly earlier than, the Shropshire specimens.

Cheirurus variolaris was founded by Linnarsson (1869 : 60, pl. 1, fig. 6) on an incomplete pygidium but later Schmidt (1881 : 183, pl. 9, figs. 1–8) illustrated the species more fully and assigned it to *Nieszkowskia*, apparently correctly, as it has a glabellar spine. The trilobite which Schmidt (1881, pl. 11, figs. 25, 26) described as *Cheirurus* (*Nieszkowskia*) *variolaris* var. *mutica* lacks a glabellar spine and is apparently a true *Acanthoparypha*. The glabellar furrows and surface tuberculation resemble those of *A. stubblefieldi* but the glabella is more transversely convex and tapered frontally than the Shropshire species. *Acanthoparypha mutica* is from Stage C 1 of Gostilizy, and is therefore of generally similar age to *A. stubblefieldi*.

Subfamily CYRTOMETOPINAE Öpik, 1937

Genus ***PSEUDOSPHAEREXOCHUS*** Schmidt, 1881

TYPE SPECIES. *Sphaerexochus hemicranium* Kutorga, 1854 by subsequent designation of Reed (1896 : 119).

Pseudosphaerexochus sp.

(Pl. 49, figs. 2, 7, 8)

1958. *Pseudosphaerexochus* sp., Dean, pp. 213, 225.

Only one specimen is available, a large but somewhat distorted cephalon approximately 60 mm. wide. The glabella is large and inflated, with a basal breadth about one-third that of the cephalon; anteriorly it expands until, at about its mid-point, it attains a maximum breadth equal to half that of the cephalon. In front of the second glabellar lobes the glabella narrows, but details are obscured by crushing. There are three pairs of glabellar furrows. The first two pairs are moderately deep at their intersection with the axial furrows, but become shallower as they curve inwards and backwards, each furrow extending adaxially for about one-quarter of the breadth of the glabella. The first and second glabellar lobes are of similar form, uniformly long (*exsag.*), and apparently parallel to each other. The third glabellar furrows are deep, directed only slightly backwards near the axial furrows; they then turn fairly sharply backwards and run towards, though they do not reach, the occipital furrow, at the same time becoming noticeably shallower. They delimit large, subangular basal glabellar lobes, each of which occupies almost one-third of the basal breadth of the glabella. The axial furrows are deep and narrow, though their narrowness may be exaggerated by crushing. The occipital furrow is narrow (*sag.*) and transversely straight, becoming deeper towards the axial furrows. The pleuroccipital furrow is deep near the axial furrows but shallows distally; towards the lateral margins it meets the lateral border furrows, demarcating a broad (*tr.*) lateral border which is continuous with the posterior border. The latter is narrow (*exsag.*) at the axial furrows but widens towards the genal angles which form broad, bluntly-pointed fixigenal spines. Only the left palpebral lobe is preserved intact, situated opposite the second glabellar lobes and about mid-way between the axial furrow and the lateral margin. It is small and short (*exsag.*), less than the length of the second glabellar lobes, with a poorly-defined palpebral furrow. The fixigenae are large, tumid and their surface is continuous with that of the librigenae. The two together are covered with conspicuous shallow pits extending as far as the lateral border furrow which separates them from the smooth lateral border, itself continuous with the distal portions of the smooth posterior border. As far as can be ascertained the surface of the glabella is smooth.

HORIZON AND LOCALITY. *Onnia* Beds, Onnian Stage, zone of *Onnia superba*, at the so-called " Cliff Section " in the north bank of the River Onny, 720 yards west-south-west of Wistanstow Church.

FIGURED SPECIMEN. BM. In. 50660.

DISCUSSION. *Pseudosphaerexochus* is figured here for the first time from Shropshire. In the Ordovician of England and Wales the genus is generally more characteristic of the Ashgill Series, though it is recorded from the Onnian and Pusgillian Stages of the Cross Fell Inlier (Dean, 1959*a*). Insufficient material is available for a detailed comparison, but the Onny specimen is larger than any of those from Cross Fell.

Family ENCRINURIDAE Angelin, 1854

Subfamily ENCRINURINAE Angelin, 1854

Genus ***ENCRINURUS*** Emmrich, 1844

TYPE SPECIES. *Entomostracites punctatus* Wahlenberg, 1821 by original designation of Emmrich (1844 : 16).

Encrinurus sp. (? nov.)

(Pl. 49, figs. 10, 12)

1958. *Encrinurus* sp., Dean, pp. 209, 223.

The single specimen available is a pygidium, strongly convex transversely and preserved as an internal mould. In outline it is almost triangular, the maximum breadth, which is attained frontally, being approximately equal to the length. The axis occupies one-third of the frontal breadth and is delimited laterally by deep axial furrows which converge gently rearwards ; it does not extend to the tip of the pygidium. There are at least sixteen or seventeen axial rings preserved, with room for a few additional rings as the axis at and near the terminal piece is slightly abraded. At least the first nine axial rings are entire, but owing to the state of preservation it is difficult to say whether the subsequent rings are obsolete mesially or whether this feature is due to abrasion. Traces of small, median tubercles are visible on the second, third, fifth, ninth, twelfth and thirteenth axial rings. Each side-lobe possesses seven well-defined ribs, with an eighth less well defined, separated from each other by conspicuous interpleural furrows which are only slightly narrower (*exsag.*) than the ribs themselves. The ribs of the first pair are transversely straight and horizontal as far as the fulcrum, beyond which they turn down and sharply back. Subsequent ribs turn backwards even more markedly, and the seventh and eighth pairs run almost straight back parallel to each other. As far as can be seen, all the ribs end in small, free points. Beyond the tip of the axis is a narrow, postaxial ridge which extends to the tip of the pygidium and is separated from the eighth pair of ribs by weak, shallow furrows.

HORIZON AND LOCALITY. The middle subdivision, the *Dalmanella unguis* Beds or Zone, of the Marshbrookian Stage, forming the upper half of the disused Marshwood Quarry, about half a mile south of Marshbrook Station.

FIGURED SPECIMEN. BM. In. 49312.

DISCUSSION. No other *Encrinurus* of comparable age or form has been described or figured from the Anglo-Welsh Caradoc Series, and the Shropshire species may be new. *Encrinurus trentonensis* Walcott (1879 : 68; Wilson, 1947: 45, pl. 8, fig. 5) has a pygidium of generally similar type but carrying at least twenty-three axial rings and nine or ten pleural ribs. This species is from the Lower Trenton of Ontario and therefore probably rather earlier than the Shropshire specimen.

Subfamily CYBELINAE Holliday, 1942

Genus ***ATRACTOPYGE*** Hawle & Corda, 1847

TYPE SPECIES. *Calymene verrucosa* Dalman, 1827 by original designation of Hawle & Corda (1847 : 90).

Atractopyge sp.

(Pl. 49, fig. 13)

1854. *Cybele verrucosa* Dalman : Salter & Aveline, p. 67.
1958. *Atractopyge* sp., Dean, p. 211.

Only one specimen has so far been collected from south Shropshire, a damaged pygidium with axis almost complete, and retaining part of the side-lobes. The maximum length, excluding the articulating half-ring, is 15 mm. The length of the axis is three times the breadth, and its sides are parallel for about two-thirds of the length but then converge to meet at the pointed axial tip. There are at least twelve axial rings, though the posterior portion of the axis is too badly damaged for more to be distinguished. The first four axial rings pass laterally without interruption into the ribs of the side-lobes, axial furrows being present merely as ill-defined, shallow, longitudinal depressions ; only to the rear of the fourth axial ring is the axis defined laterally by deep axial furrows which curve gently back to the pointed tip. The first two, and perhaps three, axial rings are entire across the median line, but all subsequent rings are obsolete medially for about one-third of their breadth (*tr.*), so that they appear to be defined by two series of transverse notches which run adaxially from just inside the axial furrows and are separated from each other by a median band which extends, apparently, to the tip of the axis. This band is mostly smooth, but the fifth to seventh, and perhaps also the fourth, axial rings bear traces of paired median tubercles. The ring furrows beyond the sixth become gradually more reduced. The first four axial rings are produced laterally to form the ribs of the side-lobes and extend transversely for a short distance from the axis ; they then curve sharply backwards and at the same time converge slightly so that the fourth pair of ribs embraces the sides of the axis and terminates in a pair of free points which almost meet just beyond its tip. The remaining ribs, from first to third, run parallel to the fourth pair and terminate in a series of free points which are not in line but are stepped adaxially rearwards from first to fourth. Each rib of the fourth pair carries a poorly-defined tubercle opposite the seventh, tenth and twelfth ring furrows, and similar tubercles are visible on the other ribs, though the preservation is too poor to ascertain their exact distribution.

HORIZON AND LOCALITY. The disused quarry by the east side of the road, almost opposite Church Farm, Acton Scott, in the Acton Scott Beds (*s.s.*), representing part of the middle third of the Actonian Stage.

FIGURED SPECIMEN. BM. In. 49319.

DISCUSSION. The name " *Cybele verrucosa* " has been applied indiscriminately for many years to specimens of *Atractopyge* from a large number of horizons and localities in Britain, and it seems probable that several different species will prove to be involved when they are better known. The true *Atractopyge verrucosa* was first described by Dalman (1827) from the Red *Tretaspis* Shales of Billingen, Västergötland, but the original illustrations were too poor for detailed comparison. More recently Henningsmoen (*in* Moore, 1959, fig. 349, 1*a*, *b*) has refigured the species from type material ; his illustration of the pygidium shows there are about eleven axial rings behind the first four entire axial ring furrows, and that the tips of the pleural ribs end almost in line with each other. This last feature marks a conspicuous difference from the Shropshire specimen, which probably also has fewer axial rings.

The species described by M'Coy (*in* Sedgwick & M'Coy, 1851 : 156, pl. 1G, figs. 1–5) as *Zethus atractopyge* has often been regarded as a synonym of *Atractopyge verrucosa*, and is certainly congeneric with the latter. *Atractopyge atractopyge* was founded on a number of syntypes in the Sedgwick Museum numbered A. 41875, A. 41903 and A. 41904*a*, *b*, deriving respectively from " Alt yr Anker, Meifod " (now Gallt-yr-Ancr), " the schists of Ravenstone Dale " (presumably the Cautley district), and " the slate of Coniston ". Of these the pygidium from near Meifod (M'Coy, fig. 4) is here chosen as lectotype, the other two being either incomplete or distorted. The hill of Gallt-yr-Ancr, near Meifod, Montgomeryshire, is made up largely of Caradoc strata belonging to the Soudleyan and Longvillian Stages. M'Coy's species is in need of redescription from topotype material and its exact type locality is, unfortunately, not known, but King (1928 : 698) has recorded " *Cybele verrucosa* " as occurring commonly at one locality on Gallt-yr-Ancr, as well as several others in the district, in company with *Pterygometopus* (now *Estoniops*) *jukesi* (Salter), a species which, so far as is known, is restricted to the Upper Longvillian Substage and is regarded here as a subjective synonym of *Estoniops alifrons* (M'Coy, 1851).

Two pygidia assigned to *Atractopyge* have been figured from the Derfel Limestone of North Wales by Whittington (*in* Whittington & Williams, 1955, pl. 40, figs. 109, 110). One of these (fig. 109) is broadly comparable with the Shropshire specimen, though the preservation is too poor for detailed comparison, but the other (fig. 110) appears to be a typical *Paracybeloides* of the *girvanensis* (Reed) species-group. As has been noted elsewhere (Dean, 1958 : 212), the association of *Atractopyge, Illaenus, Platylichas* and *Nicolella* in the Derfel Limestone is matched at a much later date in south Shropshire by part of the fauna of the Actonian Stage.

In west Shropshire Whittard (1960 : 126, pl. 17, figs. 12–16) has recorded the Scottish species *Atractopyge michelli* (Reed) from the Llandeilo Series ; the Acton Scott form can readily be separated from this species by means of its narrower, proportionately longer pygidial axis. *Atractopyge killochanensis* (Tripp, 1954 : 678, pl. 4, figs. 1–5), though broadly similar to the east Shropshire species may be distinguished by the proportionately longer axis behind the first four axial rings, and by the free points of the pleural ribs which are markedly convergent backwards.

Family DALMANITIDAE Reed, 1905

Subfamily ACASTINAE Delo, 1935

Genus ***KLOUCEKIA*** Delo, 1935

? 1956. *Dreyfussina* Choubert *et al.*, p. 394.

TYPE SPECIES. *Phacops phillipsi* Barrande, 1846 by original designation of Delo (1935 : 408).

Subgenus ***Phacopidina*** Bancroft, 1949

Phacopidina was first proposed by Bancroft (1949 : 310) as a genus of the family Phacopidae. Both Pillet (1954) and Hupé (1955 : 261) placed it in the subfamily Acastinae, using the latter as a subdivision of the Phacopidae, but since then Struve (*in* Moore, 1959 : 0.486) has preferred to assign the genus to the subfamily Calmoniinae, within the family Calmoniidae. Struve qualified this transfer by claiming that *Phacopidina* is closer to what he called " the Calmoniinae trend " on account of the direction of the second glabellar furrows, the pairs of glabellar lobes of equal size, and the shape of the genal spines. He pointed out that Bancroft's illustration of the type-species was indifferent, but his own diagram of a, presumably, mature individual of *Phacopidina harnagensis* Bancroft (Struve *in* Moore, 1959, fig. 385, 4*a*, *b*) is in turn somewhat misleading. The first glabellar furrows are too deeply impressed, the second furrows diverge forwards too strongly and are shown to reach the axial furrows, the genal spines are too short, and the facial suture is omitted. As will be described later, features approaching some of these are to be found in immature specimens of *Kloucekia* (*P.*) *harnagensis*, but in a typical adult individual the first and second glabellar lobes are fused distally, the second furrows being slightly curved, convex forwards, and not reaching the axial furrows. These characters are considered here to more in keeping with those of the subfamily Acastinae.

The Barrande Collection of Bohemian trilobites at the British Museum (Natural History) contains several specimens of *Kloucekia phillipsi* (Barrande), and examination of these has shown that the cephala of *Kloucekia* and *Phacopidina* are indistinguishable. One specimen, In. 42327, has had the genal angle developed to show the existence there of an extremely small fixigenal spine, smaller even than that of *Phacopidina*, but situated in an analogous position. The only difference between *Kloucekia* and *Phacopidina* appears to lie in the latter's possession of a mucronate pygidium, and it has been found convenient to separate the two subgenerically on this basis.

Recently the name *Dreyfussina* was proposed (Choubert *et al.*, 1956 : 394) as a subgenus of *Phacopidina*, though no adequate diagnosis or description was given. The type-species of *Dreyfussina* was originally described by Dreyfuss (1948 : 56, pl. 5, figs. 1–5, pl. 9, figs. 6, 7, 9) as *Dalmania exophtalma* from the Caradoc of the Montagne Noire in southern France. His photograph of the cephalon is indistinct and difficult to match with his line drawings in the same paper, which show the second glabellar furrows diverging forwards to cut the axial furrows. In all other respects *Dreyfussina* resembles a typical *Kloucekia* and the two may well be synonymous.

TYPE SPECIES. *Phacopidina harnagensis* by original designation of Bancroft (1949 : 310).

Kloucekia (Phacopidina) harnagensis (Bancroft)

(Pl. 49, figs. 9, 14 ; Pl. 50, figs. 1–5)

1949. *Phacopidina harnagensis* Bancroft, p. 310, pl. 10, figs. 24, 25.
1958. *Phacopidina harnagensis* Bancroft : Dean, p. 201.
1959. *Phacopidina harnagensis* Bancroft : Struve *in* Moore, p. O.486, fig. 385, 4*a*, *b*.

DESCRIPTION. The cephalic outline is sub-semicircular, bluntly pointed frontally ; the maximum breadth is almost twice the median length and is measured approximately at the line of the pleuroccipital furrow. The glabella is pentagonal in outline, expanding anteriorly to attain its maximum breadth across the frontal glabellar lobe, the apex of which is bluntly pointed ; the median length is slightly more than the breadth. The axial furrows are almost straight, diverging forwards at about 30 degrees ; they are moderately deep posteriorly, becoming shallowest anteriorly where poorly-defined hypostomal pits are sited just forwards of the first glabellar furrows. There are three pairs of glabellar lobes and furrows. The first glabellar lobes are roughly triangular in shape, slightly larger than the other glabellar lobes. The first glabellar furrows are almost obsolete ; distally they cut the axial furrows, whence they run adaxially and sharply backwards until they end longitudinally in line with the other glabellar furrows, leaving a smooth, median band. The second glabellar lobes are smaller, becoming shorter (*exsag.*) distally. They are bounded anteriorly by the second glabellar furrows which are faintly impressed, slightly curved, convex side forwards, set almost at right angles to the sagittal line, and which do not attain the axial furrows. The third glabellar furrows are deep, with apodemes, directed adaxially and slightly rearwards from the axial furrows, each extending across about one-third of the breadth of the glabella. The third glabellar lobes are subtriangular in outline, and in the internal mould they appear to constrict adaxially owing to the presence of apodemes in the occipital and third glabellar furrows. The frontal glabellar lobe is transversely lozenge-like in outline, with median length about half the breadth ; the straight, anterolateral margins converge frontally at 135 degrees, meeting at the bluntly-pointed apex. The anterior border of the cephalon is a thin, raised rim which becomes obsolete laterally, just beyond the line of the axial furrows, and is separated from the glabella by a narrow (*sag.*), moderately deep furrow containing the anterior branches of the facial suture. The lateral border furrows are represented by shallow depressions running parallel to the lateral margins and extending from the axial furrows almost to the outer ends of the pleuroccipital furrow. The distal parts of the occipital furrow are transversely straight and deep with apodemes, but the median third is much shallower and set forwards. The occipital ring is transversely convex, longest medially, becoming shorter distally where it curves forwards slightly to form a pair of small occipital lobes. The pleuroccipital furrow is set slightly to the rear of the distal ends of the occipital furrow ; it is deep and broad (*exsag.*) adaxially, and extends distally in an almost straight line, becoming shallower towards, but not reaching, the lateral margins. The posterior border is narrow (*exsag.*) immediately outside the axial furrows, but becomes markedly wider (*exsag.*) abaxially where the blunt genal angles are produced rearwards to form a pair of small, thin genal spines. The latter are situated a short distance adaxially from the lateral margins and are seldom preserved intact. The eyes are crescentic in plan, and slightly divergent backwards. Their anterior ends are sited just outside the axial furrows, opposite the anterior halves of the first glabellar lobes, and they extend back and slightly outwards until they are level with the posterior halves of the second glabellar lobes. The ocular surfaces are schizochroal and that of the lectotype, though damaged, has a total of about 115 facets on the right eye, arranged in twenty-three vertical rows. The palpebral lobes are broad (*tr.*) and horizontal, delimited adaxially by broad (*tr.*), shallow palpebral furrows, and poorly defined frontally where they extend beyond the eye as far as the axial furrows. The fixigenae decline gently from the palpebral furrows to the axial furrows, but more steeply abaxially from behind the eyes to the lateral margin. The anterior branches of the facial suture are slightly convergent forwards, where they cut the axial furrows just in front of the hypostomal pits ; they then follow the outline of the frontal glabellar lobe and meet frontally at its apex. The posterior branches curve gently forwards from the rear ends of the eyes and then slightly rearwards, cutting the lateral margins approximately in line with the third glabellar furrows.

A few immature cranidia have been found, one of which is illustrated (Pl. 50, fig. 4). They differ from those of typical adult individuals in the following respects : the glabella is slightly narrower across the third glabellar lobes, so that the axial furrows appear more divergent forwards ; the glabellar lobes decrease noticeably in size from front to rear ; the second glabellar furrows are deep and transversely straight, intersecting the axial furrows ; and the first glabellar furrows are better defined than in the adult form.

The hypostoma is unknown.

The thorax consists of eleven segments and is divided into three longitudinal lobes of approximately equal breadth by well-developed axial furrows. Each axial ring is moderately convex transversely and is curved forwards both medially and distally. The pleurae extend abaxially and horizontally for about half their length (*tr.*) as far as the fulcra, where they turn downwards through almost a right angle, at the same time curving first rearwards and then forwards slightly towards the tips, which are truncated, convergent forwards. The anterolateral part of each pleural tip is bluntly rounded, but the posterolateral part is almost a right angle, produced distally to form a small, projecting process (see Pl. 50, fig. 1) which probably functioned as a " stop " during enrolment. The proximal half of the upper surface of each pleura is horizontal, but beyond the fulcrum the distal half forms a surface which intersects the proximal half obliquely so as to form a slight ridge extending from the anterior border near the fulcrum to the posterior border just inside the pleural tip. Each pleura carries a pleural furrow which commences at the intersection of the axial furrow and the anterior border of the pleura ; the furrow then curves gently and abaxially rearwards, and finally forwards in the direction of, though without reaching, the pleural tip. The proximal half of the furrow is markedly deep, but beyond the oblique ridge near the fulcrum, as described above, it becomes markedly shallower for the remainder of its length (*tr.*).

The pygidium is broadly subparabolic in outline, its anterior margin only moderately covex, and length, excluding the terminal spine, roughly half the maximum breadth. The axis is delimited laterally by pronounced axial furrows, does not reach the posterior margin, and there are seven axial rings, of which the first four are the most clearly defined. Each side-lobe has a pronounced facet situated anterolaterally, and five ribs separated from each other by well-impressed pleural furrows and carrying fainter rib furrows. All these furrows die out laterally, leaving a smooth border. The margins of the pygidium are entire and pass posteriorly into a conspicuous, smooth spine, in length about one-third of the pygidium and rising from the axis at an angle of about 30 degrees. Behind the tip of the axis is a small postaxial ridge which merges into the base of the terminal spine.

In general the dorsal surface of the entire exoskeleton appears to be smooth but occasional well-preserved specimens show that the test, with the exception of the furrows and terminal spine, may be covered with fine, closely-set granules.

HORIZON AND LOCALITIES. The type-specimens are from the section in the disused cartway by the south-eastern corner of Smeathen Wood, 250 yards west-south-west of Wood House, five-sixths of a mile south of Horderley Station. The horizon is in the lowest part of the Harnagian Stage, the zone of *Reuscholithus reuschi*. At this locality the species is fairly abundant and is associated with *R. reuschi* Bancroft, *Smeathenia smeathenensis* (Bancroft) and *Smeathenella harnagensis* Bancroft. *Kloucekia* (*Phacopidina*) *harnagensis* occurs also, but in less abundance, at the field exposure 550 yards north-west of Woolston House, Woolston. No other localities are yet known.

LECTOTYPE, here selected. BM. In. 42089 (Pl. 50, figs. 1, 5).

PARATYPE. BM. In. 42088 (Pl. 50, fig. 3).

FIGURED SPECIMENS. BM. In. 40131 (Pl. 49, figs. 9, 14) ; BM. In. 50576 (Pl. 50, fig. 2) ; BM. In. 52211 (Pl. 50, fig. 4).

DISCUSSION. It has been found more convenient to group this section with that of *Kloucekia* (*Phacopidina*) *apiculata* (M'Coy) later in this paper (see p. 326).

Kloucekia (Phacopidina) apiculata (M'Coy)

(Pl. 50, figs. 6–10, 12)

1847. *Phacops apiculatus* MS. Sedgwick, p. 149. *Nomen nudum.*
1851. *Portlockia ? apiculata* M'Coy *ex* Salter MS., *in* Sedgwick & M'Coy, p. 162, pl. 1G, figs. 18, 19 only.
1852. *Phacops* (*Phacops*) *apiculatus* Salter, p. iii.
1853. *Phacops* (*Acaste*) *apiculatus* Salter : Salter, p. 9.
1859. *Phacops apiculatus* Salter : Murchison, p. 75, fig. 3.
1864. *Phacops* (*Acaste*) *apiculatus* Salter : Salter, p. 28, pl. 1, figs. 36–38.
1867. *Phacops apiculatus* Salter : Murchison, p. 69, fig. 3.
1924. *Dalmanitina apiculata* (Salter) : McLearn, p. 166.
1939. " *Acaste* " *apiculata* (Salter) : Stubblefield, p. 56.
1945. *Dalmanitina apiculata* (Salter) : Bancroft, p. 195.
1947. *Scotiella apiculata* (Salter) : Harper, p. 169. pl. 6, figs. 6, 9.
1949. *Phacopidina apiculata* (Salter) : Bancroft, p. 310.
1958. *Phacopidina apiculata* (Salter) : Dean, pp. 206–207, 221–222.
1959. *Phacopidina apiculata* (M'Coy) : Dean, p. 146.
1959*a*. *Phacopidina apiculata* (M'Coy) : Dean, pp. 212, 214, 220.

DESCRIPTION. The cephalic outline is almost semicircular, its length about two-thirds of the maximum breadth which is measured just in front of the pleuroccipital furrow. The glabella is pentagonal in plan, expanded anteriorly and bluntly pointed in front ; its length is about equal to, or slightly greater than, its maximum breadth. There are three pairs of glabellar furrows and glabellar lobes. The first glabellar furrows are shallow, in some cases almost obsolete, particularly adaxially, and run almost straight inwards and rearwards from the axial furrows. The first glabellar lobes are subtriangular in form, whilst the second glabellar lobes are subrectangular. The two pairs of lobes become fused distally, but proximally they are separated by shallow, slightly curved second glabellar furrows, convex forwards and set at right angles to the median line of the glabella. The third glabellar furrows, deep and with apodemes, are straight, directed inwards and rearwards from the axial furrows for about one-third of the glabellar breadth. The third glabellar lobes are subtriangular in outline, not unlike the slightly larger first glabellar lobes. All the glabellar lobes and the frontal glabellar lobe are moderately convex in line with one another. The axial furrows are almost straight, becoming slightly convex laterally opposite the first glabellar lobes ; they are shallow medially, deepening to front and rear, and inconspicuous hypostomal pits occur opposite the distal ends of the first glabellar furrows. The glabella is bounded frontally by a narrow (*sag.*) groove, representing the preglabellar furrow and field, and immediately in front of this rises the anterior border, uniformly narrow (*sag.*) and parallel to the margin of the frontal glabellar lobe. The occipital furrow is curved forwards and shallow medially, deepening laterally where a pair of apodemes is situated just inwards from the axial furrows. The occipital ring is transversely convex, longest medially but shortening (*exsag.*) distally where it curves forwards slightly so as to form a pair of occipital lobes. The pleuroccipital furrow is deep and moderately wide (*exsag.*) near the axial furrows but becomes shallower distally and finally dies out before reaching the lateral margins. The posterior border is narrow by the axial furrows but widens (*exsag.*) distally and terminates posterolaterally in a pair of almost right-angled genal angles which are produced into a pair of small, sharp fixigenal spines directed backwards and slightly outwards (see Pl. 50, fig. 6). The largest-known fixigenal spine, about 2·5 mm. long, belongs to a cephalon 11 mm. in median length.

The eyes are crescentic in plan with prominent palpebral lobes which commence at the axial furrows, immediately behind the distal ends of the first glabellar furrows, and run rearwards, curving first abaxially and then adaxially until they terminate opposite the frontal half of the third glabellar lobes and a short distance outside the axial furrows. Moderately-deep palpebral furrows run parallel to the margins of the palpebral lobes and die out as they skirt the rear ends of the eyes. The eye surfaces are schizochroal and, in the case of a cephalon 8 mm. long, each contains at least thirty-two vertical rows of up to eight facets. From the palpebral lobes the proximal surface of the fixigenae slopes steeply down to the axial furrows ; the distal surface is rather less steeply declined to the poorly-defined marginal furrows, situated just inwards from the lateral margins. The anterior branches of the facial suture are at first virtually coincident with the axial furrows, then skirt the frontal glabellar lobe and finally coalesce at the apex of the latter. The posterior branches of the suture are sigmoidal, curving gently forwards from the ends of the eyes and then backwards to cut the lateral margins opposite the mid-point of the third glabellar lobes.

The hypostoma is unknown.

No syntype thorax was available to Harper (1947) in his redescription, and only one, moderately well-preserved Shropshire specimen has been found (Pl. 50, fig. 12). This contains eleven thoracic segments and appears to agree in all essentials with the thorax of *Kloucekia* (*Phacopidina*) *harnagensis* already described (see p. 323), although full details of the pleural points cannot be distinguished. The pygidium, excluding terminal spine, is subparabolic in outline, with frontal margin moderately convex forwards. Frontally the axis occupies between one-quarter and one-third of the maximum breadth and it is bounded laterally by deep axial furrows which converge gently rearwards. A maximum of eight axial rings is present but beyond the fifth ring these are often difficult to distinguish, particularly in internal moulds. Each side-lobe is convex with an anterolateral facet, and there are five deep pleural furrows. The ribs so formed carry faintly-impressed rib furrows and these, together with the pleural furrows, do not reach the lateral margin, extending only as far as the smooth border which also defines the extent of the doublure. At the tip of the pygidium the border is produced to form a thorn-like terminal spine, directed upwards and backwards (see Pl. 50, fig. 8) and equal to almost one-third of the length of the pygidium proper. The axis extends only to the smooth border but is connected to the base of the terminal spine by a low postaxial ridge.

The surface of the exoskeleton is apparently smooth in most individuals, but occasional specimens show trances of fine granulation, at least on the surface of the cephalon.

HORIZON AND LOCALITIES. In south Shropshire *Kloucekia* (*Phacopidina*) *apiculata* is first encountered in the lowest subdivision of the Lower Longvillian Substage, the zone of *Dalmanella horderleyensis*. It then ranges upwards through the remainder of the Lower Longvillian, though not in large numbers. In the succeeding Upper Longvillian Substage the species is more abundant, although, like the remainder of the fauna, it is generally most common in calcareous bands within the large thickness of flags and sandy shales constituting the Alternata Limestone and Lower Cheney Longville Flags. In an earlier paper (Dean, 1958 : 223) *K.* (*P.*) *apiculata* was recorded from the Marshbrookian Stage, but the evidence for this was fragmentary and unsatisfactory, and it is still not known for certain whether the species occurs outside the limits of the Longvillian Stage of which it is so characteristic.

The species is to be found at numerous points along the Longvillian outcrop throughout the Caradoc District but the following may particularly be noted. *Lower Longvillian Substage:* Long Lane Quarry, two-thirds of a mile south-west of Cheney Longville ; the large road-side quarry 280 yards south-east of Glenburrell Farm, Horderley ; various exposures near the top of Rookery Wood, just south of the River Onny three-quarters of a mile south-east of Horderley ; the quarry by the east side of the road 590 yards east-north-east of Cwm Head Farm, one and a half miles north-east of Horderley. *Upper Longvillian Substage:* various exposures along Longville Lane, from 400 to 440 yards north-west of the " Earthwork " at Cheney Longville ; the old quarry below the north side of the track at the north-eastern corner of Burrells Coppice, one mile south-east of Horderley Station ; various exposures by the north side of the Bishops Castle road to the east of New House, just east of Horderley ; the stream-bed by the west side of the Horderley-Marshbrook road, 560 yards north-east of Crosspipes ; Soudley Quarry, near Soudley Pool, between Hope Bowdler and Ticklerton.

LECTOTYPE, selected by Harper (1947 : 170). Sedgwick Mus. A. 10962, a cephalon originally figured by M'Coy (*in* Sedgwick & M'Coy, 1851, pl. 1G, fig. 18) from "Caradoc Beds" near Glyn Ceiriog, Montgomeryshire, and probably of Longvillian age.

FIGURED SPECIMENS. BM. In. 32253 (Pl. 50, fig. 6) ; BM. In. 51259 (Pl. 49, figs. 7, 8) ; BM. In. 51260 (Pl. 50, fig. 9) ; BM. In. 50558 (Pl. 49, fig. 12).

DISCUSSION. *Kloucekia* (*Phacopidina*) *apiculata* is one of a number of fossil species, including also *Brongniartella bisulcata* and *B. rudis* (see p. 345), the authorship of which has usually been attributed to Salter. Salter had, in fact, prepared descriptions of some new species which were to be published as an appendix to Sedgwick & M'Coy's great work on the British Palaeozoic rocks and fossils. Publication of the appendix was delayed until July, 1852, and in the meantime M'Coy had published, in May, 1851, his own longer and more detailed descriptions, using Salter's manuscript specific names but frequently changing the genera to which they were assigned. There is no question of M'Coy's having used Salter's descriptions, and Sedgwick (*in* Sedgwick & M'Coy, 1851 : xiii–xiv) stated that "With the exception of the Appendix to the Second Fasciculus (which is from the pen of my friend and former fellow-labourer Mr. Salter) all the descriptions of the following works are due, exclusively, to Professor M'Coy . . . ". M'Coy must therefore be considered the author of the species in question. Salter's descriptions in the Appendix (1852) refer to the plates published in the preceding year and M'Coy's *Portlockia* ? *apiculata* was described by Salter as *Phacops* (*Phacops*) *apiculatus* sp. nov. The lectotype chosen by Harper is one of the specimens figured by M'Coy in 1851. The specific name as used for the first time by Sedgwick (1847 : 149) was invalid.

Although no other forms of *Kloucekia* have been found in Shropshire between *K.* (*P.*) *harnagensis* in the lower Harnagian Stage and *K.* (*P.*) *apiculata* in the Lower Longvillian Substage, nevertheless the two species appear to be closely related. They may be distinguished by the fact that *K.* (*P.*) *harnagensis* has a slightly shorter pygidium, and that the eyes of *K.* (*P.*) *apiculata* are larger and less divergent backwards. A feature common to immature individuals of both species is the lateral extension of the second glabellar furrows, which are transversely straight, to cut the axial furrows. The only other described British species of *Kloucekia*, originally *Scotiella major* (Harper, 1947 : 171, pl. 6, fig. 11), was separated by means of its short cephalon, the length of which is equal to less than half the breadth. *K.* (*P.*) *major* was described from the Lower Longvillian Substage of Caernarvonshire.

Both *K.* (*P.*) *apiculata* and *K.* (*P.*) *major* were assigned to the more typically Silurian genus *Scotiella* by Harper (1947 : 169), but recently Struve (*in* Moore, 1959 : 0.486) has maintained *Phacopidina* as a separate genus. The type species of *Scotiella* (Delo, 1935 : 409 ; 1940 : 33) is *S. logani* (Hall) from the Silurian of Nova Scotia, and differs from typical species of *Kloucekia* in the following respects : the first glabellar furrows are obsolete ; the second glabellar furrows of adult individuals cut the axial furrows; the anterior branches of the facial suture converge frontally from the eyes to the frontal lobe ; fixigenal spines are totally absent and the genal angles are rounded.

The trilobite described by Barrande (1852 : 556, pl. 26, figs. 44, 45 ; pl. 27, figs. 12–14) as *Dalmanites solitaria*, from Stage D of Bohemia, has been placed doubtfully in *Phacopidina* by Struve (*in* Moore, 1959 : 0.486, fig. 385). Struve's illustration shows the second glabellar furrows definitely cutting the axial furrows, though this is not apparent from Barrande's original figures. *D. solitaria* possesses a mucronate pygidium, and examination of a topotype specimen, BM. In. 42336, from Gross Kuchel, Czechoslovakia, suggests there is little doubt that the species is a typical *Kloucekia* (*Phacopidina*) not very different from the Anglo-Welsh species.

Phacops cf. *apiculatus* was recorded by King (*in* Wedd *et al.*, 1929 : 61) from the Ashgill Series of the Oswestry district, but the specimen in question, GSM. WK. 218, is a small pygidium of *Phillipsinella parabola* (Barrande), and it is extremely doubtful whether a true *Kloucekia* (*Phacopidina*) *apiculata* has been found higher than the Caradoc Series.

Family PTERYGOMETOPIDAE Reed, 1905

Subfamily PTERYGOMETOPINAE Reed, 1905

Genus ***CALYPTAULAX*** Cooper, 1930

The genus *Homalops* was introduced in 1884 by Remelé (p. 200), though only briefly diagnosed, and was figured by him in the following year (1885 : 25, fig. 3). Remelé's species *Homalops altumi* was redescribed later by Wiman (1907 : 130, 131, pl. 8, figs. 7–10) who considered *Homalops* to be a subgenus of *Phacops*. In the meantime Reed (1905 : 226–228) had included *Homalops* in his subfamily Pterygometopinae but had considered it to be too indifferently defined to be retained, and quoted as reference only Remelé's 1884 paper. Later Kozlowski (1923 : 29) rejected the genus on the grounds that it had never been adequately described or figured, and was apparently unaware of either Remelé's 1885 work or that of Wiman. In a later classification of the Phacopidae Reed (1927 : 352, 353) omitted all mention of *Homalops*. Wiman's more than adequate illustrations show that *Homalops* Remelé is identical with the later described *Calyptaulax* Cooper, 1930. It is clear that the name cannot, therefore, be rejected on the grounds of insufficient diagnosis, and certain Swedish material has, in fact, been referred to *Homalops* by Jaanusson (1953 : 102), but *Homalops* Remelé, 1884 is a junior homonym of both *Homalops* Burmeister, 1840 and *Homalops* Motschoulsky, 1850, and is now regarded as a subjective synonym of *Calyptaulax*.

TYPE SPECIES. *Calyptaulax glabella* by original designation of Cooper (1930 : 387).

Calyptaulax actonensis sp. nov.

(Pl. 50, figs. 11, 13, 14 ; Pl. 51, figs. 1, 2)

1958. *Calyptaulax* sp. Dean, pp. 211, 212, 224.

DIAGNOSIS. Cranidium typical of the genus. Pygidium broader than long, with six interpleural furrows, up to twelve axial ring furrows, and terminating in a blunt, upturned point.

DESCRIPTION. The glabella is depressed, roughly pentagonal in outline, its length about equal to the maximum breadth which is measured across the anterolateral margins of the first glabellar lobes. The frontal glabellar lobe is bluntly pointed frontally, alate, and extends abaxially to the anterolateral tips of the first glabellar lobes where it meets the axial furrows. There are three pairs of glabellar lobes which diminish in size from front to rear. The first glabellar lobes are long, each almost an isosceles triangle in outline ; they are delimited frontally by moderately deep first glabellar furrows which are slightly sigmoidal and widely divergent forwards. The second glabellar lobes are small, only about one-quarter the length of the first pair, and are directed abaxially rearwards parallel to the second glabellar furrows which are shallow, curved, convex forwards, directed slightly rearwards but not reaching the axial furrows, the distal third of the second glabellar lobes being fused with the first pair of lobes. The third glabellar furrows are deep, diverging posteriorly and quickly bifurcating so as to form two branches which isolate the third glabellar lobes ; the latter, slightly smaller than the second lobes, are thus present only as detached tubercles at the distal ends of the basal glabellar segment. The axial furrows are shallow, diverging forwards at 50–55 degrees for most of their length but finally becoming slightly convergent forwards around the anterior end of the first glabellar lobes. The anterior border has not been found preserved, but there appears to be a shallow preglabellar furrow bordering the anterior margin of the frontal glabellar lobe. The occipital furrow is shallow medially, deepening distally where it is flexed backwards and then abaxially so as to accommodate the posterior margins of the third glabellar lobes. The occipital ring is transversely convex, long medially becoming shorter (*exsag.*) distally where it curves forwards slightly to form a pair of ill-defined occipital lobes. Immediately outside the axial furrows the pleuroccipital furrow is moderately deep and broad (*exsag.*), delimiting the narrow (*exsag.*) posterior border which becomes still narrower distally. Neither the furrow nor the border has been found preserved beyond the line of the palpebral lobes. The fixigenae are broad and flat, bounded abaxially by well-defined palpebral furrows ; the latter appear narrow on the external mould but broader on the internal mould and extend from near the anterior ends of the first glabellar lobes to the pleuroccipital furrow. The palpebral lobes are broad, flat, level with the fixigenae and crescentic in plan. The ocular surfaces of the eyes have not been found. The anterior branches of the facial suture appear to cut the axial furrows immediately in front of the palpebral lobes ; thence they follow the anterolateral margins of the frontal glabellar lobe, converging at its apex. The posterior branches of the suture, together with the outermost parts of the fixigenae, have not been found preserved.

The hypostoma and thorax are unknown.

The pygidium is subtriangular in outline, its median length equal to two-thirds of the maximum breadth which is measured across the almost straight anterior margin ; it tapers to a blunt, slightly upturned point, the extreme tip of which has not been seen intact. The axis occupies just less than one-third of the frontal breadth of the pygidium and its sides converge rearwards for about two-thirds of their length, after which they continue almost parallel to the tip of the axis. Owing to the state of preservation, in a sandstone, of the holotype pygidium only eight axial rings are visible but other specimens, found in a fine-grained argillaceous matrix, have eleven or twelve rings. The axial rings themselves are slightly sigmoidal in plan, curving back both medially and distally. Beyond the tip of the axis is a low, smooth, postaxial ridge which runs into the terminal point. On each side-lobe of the pygidium there are six well-defined interpleural furrows ; these decrease in depth from first to sixth and extend about two-thirds of the distance from the axial furrow to the lateral margin, apparently ending in line with the inner margin of the doublure. An equal number of rib-furrows is present, each commencing about one-third of the distance from the axial furrow to the lateral margin and then turning rearwards markedly until it intersects the margin. The first pair of rib-furrows is deeply defined, but the remainder become progressively fainter towards the tip of the pygidium. A well-developed facet is present anterolaterally on each side-lobe, immediately in front of the first rib-furrow.

Fragmentary evidence suggests that the surface of the test of both glabella and pygidium, excepting the furrows, is covered with fine, evenly-distributed granules.

HORIZONS AND LOCALITIES. The type-locality is the site of the old quarry, now filled in, at Quarry Field, Gretton, half a mile east of Cardington. The horizon is in decalcified sandstones belonging to the middle third of the Actonian Stage. The species has also been found in the disused quarries 80 yards south-east and 250 yards east of St. Margaret's Church, Acton Scott. At one time *Calyptaulax actonensis* was thought to occur only in the middle Actonian of south Shropshire (Dean, 1958 : 211), but whilst it is still true that the species is most abundant at this level, it has now been found in the lowest Actonian strata at the large exposure in the south bank of the River Onny about 85 yards west of its junction with Batch Gutter stream, and also in the topmost Actonian and basal Onnian beds exposed in the north bank of the Onny about 30 yards east of the same river/stream junction. Specimens are rare at these latter localities and have not been found higher in the succession.

HOLOTYPE. BM. In. 49771 (Pl. 50, figs. 11, 14).

PARATYPES. BM. In. 48492 (Pl. 50, fig. 13) ; BM. In. 49318 (Pl. 51, fig. 1) ; BM. In. 49768 (Pl. 51, fig. 2).

DISCUSSION. *Calyptaulax* is a predominantly North American trilobite genus and is figured here for the first time from Shropshire. *C. actonensis* bears some resemblance to *C. altumi* as figured by Wiman (1907, pl. 8, figs. 7–10) but differs in having slightly wider fixigenae and a longer pygidium. I am indebted to Dr. Valdar Jaanusson of Uppsala University for the opportunity of comparing my Shropshire specimens with material collected from a South Bothnian drift boulder and determined by Professor Wiman as *C. altumi* (Remelé). Dr. Jaanusson kindly informs me these specimens are derived from strata belonging to the zone of *Pleurograptus linearis*, that is to say, beds younger than those of south Shropshire which belong to the zone of *Dicranograptus clingani*

The cranidium of the Norwegian species *Calyptaulax norvegicus* (Størmer, 1945 : 417, pl. 4, figs. 2, 3) is virtually indistinguishable from that of *C. actonensis*, but the pygidium differs in having a narrower, more uniformly tapered axis with slightly longer (*sag.*) axial rings. In outline the pygidium of the new species resembles that figured by Jaanusson (1953 : 103, fig. 4) as *Homalops* cf. *altumi* Remelé from the Slandrom Limestone of Dalarne, a horizon belonging to the zone of *Pleurograptus linearis* but containing, nevertheless, a fauna resembling in many respects that of the Actonian Stage in South Shropshire. The Swedish pygidium is incomplete but appears to have fewer axial rings and, probably, rib-furrows.

Under the name " Subgenus A " Struve (*in* Moore, 1959 : 0.491, 492) has recently separated from *Calyptaulax* (*s.s.*) a cranidium of *Calyptaulax altumi* from a Pleistocene erratic in Sweden, together with the pygidium recorded from the Slandrom Limestone by Jaanusson as *Homalops* cf. *altumi* and noted above. The latter pygidium compares closely with that of *C. actonensis*, a species which, in turn, possesses a cranidium indistinguishable, even subgenerically in the writer's opinion, from the type-species of *Calyptaulax*. According to Struve's illustration the cranidium of " Subgenus A " possesses palpebral lobes which become markedly narrow frontally and second glabellar lobes which are present only as detached tubercles. These features may possibly merit subgeneric separation but they have not yet been fully investigated and are not, in fact, present on the specimens of *C. altumi* lent by Dr. Jaanusson, which are best grouped with *Calyptaulax* (*s.s.*). *Calyptaulax compressa* (Cooper, 1930, pl. 5, figs. 7, 8) has a shorter glabella and smaller fixigenae than *C. actonensis*, whilst *C. glabella* (Cooper, 1930, pl. 5, figs. 9–11) has only nine well-defined axial rings on the pygidium. *C. schucherti* Troedsson (1929, pl. 19, figs. 17–20) from the Cape Calhoun Formation of Greenland may be distinguished from the Shropshire species by its shorter frontal lobe and smaller fixigenae and first glabellar lobes.

Subfamily CHASMOPSINAE Pillet, 1954

Genus ***CHASMOPS*** M'Coy, 1849

TYPE SPECIES. *Calymene odini* Eichwald, 1840 by original designation of M'Coy (1849 : 403).

Chasmops extensa (Boeck)

(Pl. 51, figs. 3–10 ; Pl. 52, figs. 1, 3, 4, 6, 7)

1838. *Trilobites extensus* Boeck, p. 139.
1839. *Asaphus Powisii* Murchison, p. 661, pl. 23, fig. 9*a* and *b* only.
1848. *Dalmania affinis* Salter, p. 337, pl. 5, fig. 5.
1849. *Phacops truncato-caudatus* var. β, *affinis* Salter, p. 7.
1851. *Odontochile truncato-caudata* (Portlock) M'Coy *in* Sedgwick & M'Coy, p. 162, pl. 1G, figs. 20, ? 21.
1853. *Phacops conophthalmus* (Boeck) : Salter, pp. 7, 11.
1854. *Phacops conophthalmus* (Boeck) : Murchison, pl. 4, figs. 11, 12.
1854. *Phacops conophthalmus* (Boeck) : Salter & Aveline, p. 67.
1854. *Phacops truncato-caudatus* (Portlock) : Salter & Aveline, p. 67.
1859. *Phacops conophthalmus* (Boeck) : Murchison, pl. 4, figs. 11, 12.
1864. *Phacops* (*Chasmops*) *macroura* Sjögren : Salter, p. 37, pl. 4, figs. 18–23.
1864. *Phacops* (*Chasmops*) *conophthalmus* Boeck? (pars), Salter, p. 40, pl. 4, fig. 24.
1867. *Phacops conophthalmus* (Boeck) ; Murchison, pl. 4, figs. 11, 12.
1872. *Phacops conophthalmus* (Boeck) : Murchison, pl. 4, figs. 11, 12.
1884. *Phacops conicophthalmus* (Boeck) : La Touche, p. 57, pl. 3, figs. 65, 65*a*.
1884. *Phacops macroura* Sjögren : La Touche, p. 57, pl. 3, fig. 66.
1938. *Chasmops* cf. *macroura* (Sjögren) : Stubblefield *in* Pocock *et al.*, pp. 90, 255.
1940. *Chasmops extensa* (Boeck) : Størmer, p. 138, pl. 4, figs. 7–11.
1945. *Chasmops macroura* (Sjögren) : Bancroft, p. 183.
1953. *Chasmops extensa* (Boeck) : Størmer, pp. 65, 68–69, 87, 130, 134.
1958. *Chasmops* sp., Dean, pp. 222–224.
1959*a*. *Chasmops extensa* (Boeck) : Dean, p. 221.

DESCRIPTION. The cephalon is longitudinally and transversely convex with median length almost three-fifths of the maximum breadth. The glabella is large, almost subpentagonal in outline, strongly convex, its length about three-quarters of the maximum breadth measured across the frontal glabellar lobe. There are three pairs of lateral glabellar lobes. The first glabellar furrows diverge forwards at about 110 degrees ; at their mid-points they are slightly concave forwards but abaxially they curve sharply backwards through almost a right angle, becoming deeper and finally cutting the axial furrows. The first glabellar lobes are extremely large by comparison with the other pairs of lobes ; they are roughly triangular in plan, expanding enormously in length (*exsag.*) from just in front of the second glabellar lobes and indenting the frontal glabellar lobe posterolaterally. Behind the first glabellar lobes a pair of deep furrows extends adaxially, finally bifurcating to form the second and third glabellar furrows which appear then as notches delimiting, both frontally and posteriorly, the small tubercle-like projections which serve as second glabellar lobes. Third glabellar lobes are represented by the slightly curved-forwards, posterolateral extremities of a basal glabellar segment which extends abaxially almost to the posterior ends of the first glabellar lobes. When preserved as internal moulds the third glabellar lobes appear as almost detached, rounded, knob-like projections. The frontal glabellar lobe is large, strongly convex, and broadest frontally where the breadth is about twice the length. Occasionally, cephala of *Chasmops extensa* preserved as internal moulds exhibit a V-shaped group of tubercles, directed backwards and extending from the preglabellar furrow to a position opposite the frontal portion of the first glabellar lobes. This structure was noted in specimens from Shropshire by Salter (1864 : 39, pl. 4, fig. 20), and a similar feature has been figured by Harrington (*in* Moore, 1959, fig. 69E) for *Chasmops odini* (Eichwald) from Estonia and termed " auxiliary impressions ", the exact function of which is not yet clear. Schmidt (1881, pl. 2, figs. 2, 3, 10 ; pl. 5, figs. 1, 9) has figured analogous structures in other species of *Chasmops*. The frontal margin of the frontal glabellar lobe is indented medially by a deep, broad (*sag.*) preglabellar furrow which curves gently forwards and then slightly backwards abaxially, at the same time becoming shallower and almost dying-out where it meets the axial furrows. The latter diverge forwards at an average angle of about 40 degrees but are laterally convex in part so as to accommodate the distal margins of the first glabellar lobes ; they are generally deep and narrow but become markedly shallower medially, just to the rear of centre of the first glabellar lobes. The preglabellar field is convex, becoming thicker medially, coincident with the concave margin of the frontal glabellar lobe ; distally it narrows (*exsag.*) slightly, and then maintains a uniform breadth along the anterior margin of the frontal glabellar lobe, finally curving around the tips of the latter to meet the axial furrows. The anterior border furrow is narrow (*sag.*) frontally, becoming broader and shallow abaxially where it curves sharply backwards to intersect the axial furrows. The anterior border is uniformly convex forwards in plan and has a flattened upper surface declined frontally ; the breadth (*sag.*) is generally uniform but at the line of the axial furrows it expands to form V-shaped projections extending into the anterior parts of the axial furrows themselves. Beyond the axial furrows the border narrows (*exsag.*) again and is separated from the fixigenae by broad (*tr.*), moderately-deep lateral furrows which extend rearwards to meet the distal ends of the pleuroccipital furrow. The occipital ring is long (*sag.*), transversely convex but flattened longitudinally, curving forwards distally to form a pair of large occipital lobes which are poorly defined laterally by the ends of the axial furrows. The occipital ring is bordered frontally by a deep, uniformly broad (*sag.*) occipital furrow. The pleuroccipital furrow is deep and broad (*exsag.*), curving rearwards slightly distally where it intersects the shallower lateral border furrows without reaching the lateral margins. The posterior border is narrow (*exsag.*) immediately outside the axial furrows, becoming still narrower mid-way to the lateral margins and then expanding rapidly towards the genal angles which are produced backwards to form large fixigenal spines. The latter are about as long as the cephalon (*sag.*) and their upper surface is flattened, declined distally at almost a right angle ; the lateral margins are longitudinally straight and the proximal margins run abaxially backwards to meet them and form pointed tips. The smaller, proximal halves of the fixigenae decline steeply from the palpebral lobes to the axial furrows ; the distal halves are plump, quadrant shaped, and steeply declined to the lateral border furrows. The schizochroal eyes are semicircular in plan, standing higher than the median lobe of the glabella ; they are highest medially, becoming lower both anteriorly and posteriorly, and the visual surface is steeply declined abaxially. The eyes are not generally preserved whole, but the left eye of a cephalon, In. 52166, with a median length of 32 mm. possesses 350 facets arranged in twenty-nine vertical rows containing from four to sixteen facets. Immediately below each eye there is a broad, pronounced eye platform, as long as and parallel to the visual surface. The palpebral lobes are broad, strongly convex distally in plan, steeply declined adaxially and delimited by deep, broad palpebral furrows. Each palpebral furrow follows an outwardly-directed, V-shaped course above the apex of the eye, curving around both ends of the eye to join the eye-platform below. The anterior branches of the facial suture run almost straight forwards from the eyes, cutting first the eye-platforms near their anterior ends, crossing the fixigenae, and cutting the axial furrows mid-way between the distal ends of the first glabellar furrows and the lateral extremities of the frontal glabellar lobe ; they follow the axial furrows forwards and then curve sharply adaxially, first cutting the preglabellar field and finally coinciding with the anterior border furrow until they meet frontally. The posterior branches of the facial suture are placed in shallow grooves suggestive of those found in the other phacopid genera *Pterygometopus* and *Estoniops*, and run abaxially from the rear ends of the eyes, at first almost straight, cutting the eye-platforms ; they then curve gently forwards and, finally, more markedly rearwards, meeting the lateral margins at a sharply acute angle.

The surface of the glabella and, to a lesser degree, of the occipital ring is covered with scattered, coarse tubercles each of which, on magnification (see Pl. 52, fig. 6), is seen to comprise a cluster, generally about fifteen to twenty-five, of smaller granules. Granules of similar size are thinly distributed between the tubercles, and become still sparser across the proximal ends of the first glabellar lobes. The surface of the preglabellar field is conspicuously distinct from that of the glabella, being covered with closely-set, uniformly distributed granules (Pl. 52, fig. 1). A similar ornamentation is found on the test of the anterior border (not preserved in Pl. 52, fig. 1) and extends posterolaterally along the lateral borders. The proximal surface of the librigenae is similar to that of the glabella, but the tubercles are less well defined. The test of the posterior border is finely granulate, particularly the anterior half which appears almost smooth. Abaxially all the granules disappear and the test of the genal spines is quite smooth. The deepest parts of all the cephalic furrows, together with the proximal parts of the eye-platforms, are also smooth.

The hypostoma, rarely found unbroken, is roughly triangular in plan, its maximum breadth, measured across the anterior wings, approximately equal to, or slightly less than, the median length. The anterior border, barely differentiated from the median body, is rounded, convex forwards, and continuous in line with the anterior wings which form conspicuous lateral projections and are twisted through almost a right-angle near their tips. A short distance behind the anterior wings is a pair of ill-defined projections which probably represent attenuated posterior wings. The lateral border is narrow, passing into the posterior border which forms a flattened, bluntly pointed, spatulate extension occupying almost one-quarter of the median length of the hypostoma. The median lobe is moderately tumid, about three-quarters of the total length, narrowing rearwards where it is delimited by the transverse median furrow. The last-named is almost obsolete medially but deepens laterally where it runs forwards to meet the lateral border just to the rear of the anterior wings. Immediately behind, and parallel to, the transverse median furrow is a narrow posterior lobe, poorly defined medially but expanding laterally and forwards to give rise to a pair of oblique maculae sited opposite and just to the rear of the posterior wings. A shallow, posterior transverse furrow, also parallel to the transverse median furrow, separates the posterior lobe from the posterior border and becomes deeper laterally and forwards. A few better-preserved specimens show traces of coarse tubercles on the ventral surface of the median lobe.

The thorax is known so far from only a few incomplete segments, none of which has the tips preserved. Each axial ring is of similar size to the occipital ring, being transversely broad and convex but longitudinally flat ; the anterior and posterior margins are, for the most part, transversely parallel except near the deep axial furrows where the distal portions curve forwards slightly to form a pair of small lobes. The articulating half-ring is large, about two-thirds the length (*sag.*) of the axial ring, from which it is separated by a deep, narrow (*sag.*) articulating furrow. Each pleura is of uniform breadth (*exsag.*), equal to that of the axial ring, as far as the fulcrum, beyond which point its form is not known. A deep, narrow (*exsag.*) pleural furrow commences at the junction of the anterior margin with the axial furrow, then curves gently and abaxially back as far as the fulcrum where it begins to curve forwards again, its subsequent course being unknown.

The pygidium is large, elongate, subparabolic in outline, its anterior margin only gently convex forwards. Strongly arched transversely, and gently declined posteriorly, it terminates in a bluntly-pointed, slightly upturned tip. Frontally the axis occupies about one-third of the projected breadth, is straight-sided, and tapers uniformly rearwards, extending for about five-sixths of the length of the pygidium. The axial furrows are, for the most part, well defined but become obsolete near the end of the axis which passes into a transversely convex postaxial ridge extending to the tip of the pygidium. The largest available specimen, about 36 mm. long, has sixteen axial rings which do not reach the tip of the axis. The ring-furrows are generally well defined, becoming less so after about the twelfth, and some of the first few axial rings have their posterior margins indented medially, revealing what would be the corresponding articulating half-ring on the unfused segments of the thoracic axis (see Pl. 51, figs. 5, 7). Each side-lobe carries up to sixteen ribs which become progressively less transverse in direction from front to rear until the final rib is parallel to the sagittal line. The ribs are separated by deep, narrow (*exsag.*) pleural furrows which are gently sigmoidal in plan and become almost obsolete at what is probably the inner margin of the doublure, so that an almost smooth border results. The hindmost pleural furrows are fainter than the rest and the final pair encroaches upon the sides of the postaxial ridge which may, in consequence, have a slightly waist-like appearance. Each rib is divided into two almost equal bands by a faint interpleural furrow which commences at the junction of the posterior margin of the rib with the axial furrow (see Pl. 52, fig. 7) and does not extend so far distally as do the adjacent pleural furrows. The pygidial margin is entire, arched upwards strongly at the tip. The surface of each axial ring is covered with fine, evenly-distributed granules at and near the sagittal line. Similar granules cover the surface of the posterior band of each rib but tend to die away on the anterior band (see Pl. 52, fig. 7). The border and postaxial ridge are also finely granulate but the axial furrows and articulating furrow are quite smooth.

HORIZONS AND LOCALITIES. The earliest known specimens of *Chasmops extensa* in south Shropshire have been collected from the upper portion of the Upper Longvillian Substage, the Lower Cheney Longville Flags. At this horizon *C. extensa*, though not abundant, is found in association with *Kjaerina typa* Bancroft, *Dolerorthis duftonensis* (Reed) and *Kloucekia* (*Phacopidina*) *apiculata* (M'Coy). It may be found at a number of localities along the River Onny Valley, about a mile south-east of Horderley Station, and along Longville Lane, between 35 and 120 yards north-west of the Earthwork at Cheney Longville.

The species is more abundant in the Marshbrookian Stage, or Upper Cheney Longville Flags, particularly the lowest two-thirds. At this horizon it is to be found throughout much of the Caradoc Area, the most prolific localities including : the Onny Valley east of Burrells Coppice, south-east of Horderley ; the exposure 250 feet north-north-east of Woolston House, Woolston ; numerous exposures in the vicinity of Marshbrook, including the well-known Marsh Wood quarry ; and the stream-section 550 yards south-south-west of Common Farm, Wallsbank.

Chasmops extensa occurs sporadically throughout the mudstones of the Actonian Stage in the Onny Valley, north-east of Cheney Longville, certain levels being occasionally marked by an abundance of individuals. Some of these may attain a large size and frequently have the test preserved. Northwards from the Onny the species is to be found at many places where the Actonian Stage crops out, but generally tends to be less abundant in the arenaceous rocks of the Stage. Localities include : the south bank of the River Onny about 80 yards west of its junction with Batch Gutter stream ; the upper reaches of Batch Gutter itself, half a mile north-west of Wistanstow ; various quarries in the vicinity of Acton Scott village ; exposures around the village of Plaish, 5 miles north-east of Church Stretton ; and the old quarry (now filled in) at Gretton, half a mile east of Cardington. The last two of these are in the arenaceous development of the Acton Scott Beds, probably representing the middle part of the Actonian Stage.

The stratigraphically youngest specimens of *Chasmops extensa* in south Shropshire are known from the lowest zone of the Onnian Stage in the Onny Valley, in association with *Onnia*? *cobboldi* (Bancroft). A typical locality is in the north bank of the river 35 yards east of its junction with the stream of Batch Gutter.

FIGURED SPECIMENS. BM. In. 49126 (Pl. 51, fig. 6) ; BM. In. 49127 (Pl. 51, figs. 4, 8, 10 ; Pl. 52, figs. 1, 6) ; BM. In. 49128 (Pl. 51, figs. 5, 9 ; Pl. 52, fig. 7) ; BM. In. 50546 (Pl. 51, fig. 7) ; BM. In. 50547 (Pl. 51, fig. 3) ; BM. In. 50548 (Pl. 52, fig. 4) ; BM. In. 50549 (Pl. 52, fig. 3).

DISCUSSION. *Chasmops extensa* was first introduced as a species by Boeck (1838) but the name was allowed to lapse from general usage until revived more recently by Størmer (1940 : 138) who has figured the lectotype from Gaasøen, near Oslo. In southern Norway the species is characteristic of the Upper Chasmops Shale (4bγ) and the Upper Chasmops Limestone (4bδ), a vertical range broadly comparable with that found in south Shropshire. It has been suggested by Størmer that *Chasmops macroura*, from Sweden, may be synonymous with *C. extensa*, but the problem is not yet resolved owing to lack of detailed information on the type specimen of *C. macroura*. The Swedish species was first described and figured by Angelin (1854 : 9, pl. 7, figs. 3, 4) but he attributed the name to Sjögren who has since been generally accepted as its author. Howell (1951 : 299) has pointed out that no evidence exists to show that Sjögren's was anything more than a manuscript name and Angelin must accordingly be considered the author.

The material from the Lower Cheney Longville Flags of Shropshire agrees well with Størmer's illustrations of the lectotype of *C. extensa*, and the Shropshire specimens from this horizon are only slightly larger. Specimens from the Actonian Stage of the Onny Valley frequently attain much larger dimensions but this is not considered to be more than a local variation, perhaps the result of a more favourable environment.

Warburg (1925 : 402) considered *Chasmops maxima* (Schmidt, 1881 : 112) to be identical with *C. macroura*, but according to Størmer (1945 : 421) the former may justifiably be regarded as a distinct species on account of the longer, deeper axial furrows of the pygidium. The specimens, including the pygidium, of *C. maxima* illustrated by Størmer (1945, pl. 2, figs. 1–5) show such a strong resemblance to *C. extensa* that the former may well be no more than a subspecies or variety of the latter, if not actually conspecific with it.

Salter (1864 : 41) recorded what he called " *Phacops* (*Chasmops*) *conophthalmus* (sic) Boeck " from the Caradoc Series of " Acton Scott ". This species, the lectotype of which has been refigured by Størmer (1940, pl. 3, figs. 1–6), is more correctly called *Chasmops conicophthalma* (Sars & Boeck), and is characteristic of the Lower Chasmops Shale (4bα) and the Lower Chasmops Limestone (4bβ) in southern Norway. One of the most conspicuous differences between this species and *C. extensa* is the former's possession of a short, rounded pygidium, contrasting with the elongated pygidium of the latter species. Specimens of *Chasmops* with somewhat similar, short pygidia have been collected from the Lower Longvillian Substage of the Cross Fell Inlier and North Wales, but as far as is known no genuine *C. conicophthalma* has yet been recovered from the Caradoc of Great Britain.

Chasmops amphora was founded by Salter (1853 : 12 ; 1864 : 42, pl. 4, fig. 16) on a large pygidium from the Crûg (= Crugg or Grug) Limestone of the Llandilo district of South Wales, a horizon stated by Williams (1953 : 195) to be Longvillian to Marshbrookian in age. The associated fauna includes *Atractopyge*, *Illaenus*, *Leptaena*, *Nicolella* and *Onniella* ?, an assemblage which suggests that the limestone, at least in part, might well prove to include strata as high as Actonian in age. At all events, *C. amphora* appears to be generally contemporaneous with *C. extensa* as found in Shropshire. An undoubted cephalon of *C. amphora* has apparently never been figured, but cranidia of *Chasmops* recently obtained from the Crûg Limestone are remarkably close to those of *C. extensa* and it is therefore possible that the two species may occur in association, though the pygidium of the latter species has yet to be found in South Wales. The pygidium of *C. amphora* is easily recognized by its tumid form which is more strongly arched, both longitudinally and transversely, than that of *C. extensa*, by its more rounded tip, and by the pleural furrows which, on the holotype at least, appear to be pitted and which are more strongly defined both at and across the otherwise smooth border.

Chasmops salopiensis sp. nov.

(Pl. 52, figs. 2?, 5)

Diagnosis. Glabella of distinctive shape, triangular in plan, narrowing backwards markedly to small occipital ring. First glabellar lobes small. Frontal glabellar lobe large, long, about two-thirds median length of glabella.

Description. The cephalon is roughly semicircular in outline, its median length less than half the maximum breadth. The glabella is moderately convex, both longitudinally and transversely, broader than long in the ratio of about 3 : 2, and roughly triangular in outline. It is bounded abaxially by almost straight axial furrows which diverge forwards at about 55 degrees; these become shallower medially, where they are constricted slightly opposite the first and second glabellar furrows. The frontal glabellar lobe is large, alate, subtriangular in outline, about twice as broad as long, and occupying more than half the median length of the glabella. The first glabellar furrows are deep, almost straight, and diverge anteriorly at 125 degrees; the first glabellar lobes, each roughly the shape of an isosceles triangle, occupy one-third of the length of the glabella, and are connected to the central lobe of the glabella by narrow " necks ". The second glabellar furrows are short (*tr.*), deep, and converge anteriorly at about 70 degrees; second glabellar lobes are sited at the distal ends of the second furrows and are represented by a pair of small tubercles, one at either end of a poorly-defined glabellar segment. The third glabellar furrows are barely visible small notches, and the third glabellar lobes are formed at the abaxial extremities of a small, basal glabellar segment which is slightly more conspicuous than that immediately in front. The occipital furrow is transversely straight, of moderate depth medially but becoming deeper abaxially where it ends in a pair of deep apodemal pits. The occipital ring is incompletely known, but is small, transversely convex, and apparently of small size. The posterior median lobe of the glabella is conspicuously narrow, equal to only one-sixth of the maximum breadth of the frontal glabellar lobe. The preglabellar field, though not conspicuous, is best developed medially, becoming narrower (*exsag.*) abaxially where it follows the outline of the frontal glabellar lobe until it is truncated by the axial furrows. Frontally the preglabellar field is delimited by a shallow, narrow (*exsag.*) anterior border furrow which runs parallel to the preglabellar furrow until it intersects the axial furrows. The anterior border is narrow (*sag.*), reflexed so as to produce a bluntly-rounded cross-section, and broadens (*exsag.*) distally where it passes without interruption into the lateral border. The latter is delimited by deep, broad lateral border furrows which run parallel to the lateral margin from the axial furrows. The posterior border furrows are narrow (*exsag.*) and moderately deep towards the axial furrows, but they widen abaxially and finally intersect the lateral border furrows. Near the axial furrows the posterior border at first narrows (*exsag.*) and then becomes parallel-sided, but at the posterolateral angles it increases in size abruptly and is produced rearwards to form a pair of large, tapering fixigenal spines. The upper surface of each spine is steeply declined outwards, its abaxial margin continuous with that of the lateral borders, and the length of each spine is at least equal to that of the cranidium at the sagittal line.

The proximal parts of the fixigenae are narrow and declined steeply from the palpebral lobes to the axial furrows ; they are surmounted by conspicuous, reniform, palpebral lobes set high above the level of the glabella and separated from the fixigenae by broad, well-defined, palpebral furrows. The schizochroal eyes are large, their visual surfaces steeply declined distally, and they extend from points in line with the adaxial ends of the first glabellar furrows until they are opposite the third glabellar lobes. The visual surface of the right eye of the holotype is partly preserved, though slightly displaced from its normal position. At least fifteen vertical rows of facets are visible as far as the mid-point of the palpebral lobe, so that about thirty rows must originally have been present. The number of facets in each row, as far as can be judged, varies from five to thirteen. The anterior branches of the facial suture run almost straight forwards from the eyes to cut the axial furrows, diverge forwards around the distal ends of the frontal glabella lobe, and finally converge to meet frontally, their course beyond the axial furrows almost coinciding with that of the anterior border furrow. The posterior branches run outwards from the eyes, arching first forwards and then rearwards until they cut the lateral border at an acute angle roughly in line with the third glabellar lobes. Immediately below each eye, and equal in length to the latter, is a well-defined, level, eye platform from which the main convex part of the librigena is steeply declined as far as the lateral border furrow.

The surface of the test of the glabella and fixigenae is only partly known but most of it, at least, is ornamented with what appear to be large dispersed tubercles. As in the case of *Chasmops extensa* (see p. 333) each of these is seen, on magnification, to consist of a group of closely-packed, smaller granules, others of which are dispersed over the intervening spaces. The surface of the preglabellar field, anterior border and lateral border is granulate, but that of the various cephalic furrows and the genal spines is smooth.

The hypostoma and thorax are not known.

One fairly complete pygidium of *Chasmops* has been found in association with the holotype cephalon of *C. salopiensis* and may belong to the species. It is subparabolic in outline and, in spite of some crushing, is apparently strongly convex transversely.

and about as long as broad. The axis, which carries sixteen axial rings, is bounded laterally by deep axial furrows along the whole of its length. In plan the axis tapers gently, ends in a bluntly rounded tip, and does not extend the whole length of the pygidium, being followed posteriorly by a small postaxial ridge. Each side-lobe carries sixteen ribs, the hindmost of which are only poorly defined. The ribs are separated by moderately deep pleural furrows which extend uniformly abaxially as far as the inner margin of the doublure, when they become suddenly shallower and fainter, at the same time curving back to the lateral margins. The pairs of ribs become progressively less divergent rearwards until the final, poorly-defined pair runs almost parallel to, and delimits, the postaxial ridge. The test of the pygidium is imperfectly known, but near the lateral margin appears to be finely granulate.

Horizon and locality. The specimens described were collected from a 3-inch band containing fragmentary trilobites and brachiopods in the north bank of the River Onny, about 30 yards east of its junction with the stream from Batch Gutter. The associated fauna includes *Platylichas*, *Remopleurides*, *Tretaspis*, *Onniella* and *Sampo*. The horizon is in the topmost part of the Actonian Stage and the species has not yet been found elsewhere.

Holotype. BM. In. 50551 (Pl. 52, fig. 5).

Discussion. *Chasmops salopiensis* is probably most closely related to *C. extensa* but its cephalon may be distinguished by its longer and proportionately larger frontal glabellar lobe, the smaller first glabellar lobes, the narrower posterior portion of the glabella with its smaller occipital ring, and by the straighter axial furrows.

The pygidium which is tentatively assigned to the new species appears to have a narrower axis than that of *C. extensa*, but the specimen is not well preserved and so has not been included as type-material.

Family Homalonotidae Chapman, 1890

Genus ***PLATYCORYPHE*** Foerste, 1919

Some of the south Shropshire trilobites now assigned to *Platycoryphe* have been referred previously to *Eohomalonotus* Reed, 1918. The latter genus, together with *Calymenella* Bergeron, 1890, has been discussed by Prantl & Přibyl (1948) and Sdzuy (1957). The former authors regarded *Calymenella* as a subgenus of *Eohomalontus*, whilst the latter author believed the reverse to be true on the grounds that *Calymenella* was the earlier described genus. Sdzuy's views have since been reiterated (*in* Moore, 1959 : 0.484). The evidence for separating *Calymenella* and *Eohomalonotus* seems to be tenuous and Whittard (1960 : 162) regards them as synonymous, but both are typically genera differing markedly from the south Shropshire forms; certain of the latter are, in turn, remarkably close to the type-species of the North American genus *Platycoryphe*. Recently this name has been placed by Henningsmoen (*in* Moore, 1959 : 0.524) with the trilobites whose Order and Family are doubtful, but Whittard (1961 : 163) has used it to include certain Ordovician Homalonotidae from the Shelve Inlier, west Shropshire, and it is regarded here as being best grouped with

Calymenella and related genera. *Platycoryphe* is recorded from such widely-scattered regions as Bohemia, Shropshire and eastern North America, all the known occurrences being of Middle or Upper Ordovician age.

Platycoryphe dentata sp. nov.

(Pl. 53, figs. 1–7, 9, 13 ; Pl. 55, figs. 3, 10)

1854. *Homalonotus rudis* M'Coy : Salter & Aveline, p. 65.
1865. *Homalonotus rudis* M'Coy : Salter, pl. 10, fig. 11.
1865*a*. *Homalonotus rudis* M'Coy : Salter, pl. 10, fig. 13.
1873. *Homalonotus rudis* M'Coy : Salter, p. 53.
1918. *Homalonotus biserratus* (*pars*). Reed, p. 273. MS. name only.
1938. " *Homalonotus* " cf. *bohemicus* Barrande : Stubblefield *in* Pocock *et al.*, p. 255.
1939. *Eohomalonotus*? cf. *bohemicus* (Barrande) Stubblefield, p. 55.
1958. *Eohomalonotus* sp., Dean, p. 218.

DIAGNOSIS. *Platycoryphe* with three well-defined pairs of glabellar lobes. Distinct paraglabellar areas present. Tumid pygidium with six or seven axial rings and five pairs of pleural ribs. Each rib terminates laterally in two tooth-like projections, the anterior of which is the larger, separated from each other by the interpleural furrow.

DESCRIPTION. The cranidium is moderately convex transversely, less convex longitudinally, with a maximum breadth generally about equal to its basal breadth, but two, probably dimorphous, forms of the species are present and in the second of these the glabella is conspicuously narrower (see Pl. 53, figs. 3, 9). Such a feature may possibly be of sexual significance. The glabella is gently convex, subtrapezoidal in outline, with three pairs of well-defined glabellar lobes. The frontal glabellar lobe is subquadrate in plan with a slightly convex anterior margin and occupies between one-quarter and one-third of the median length of the glabella. The first glabellar furrows are shallow, gently curved, convex forwards, and extend adaxially and slightly rearwards from the axial furrows for about one-quarter of the glabellar breadth. The first glabellar lobes are subquadrate, equal to about one-sixth of the length of the glabella ; they are bounded to the rear by the second glabellar furrows which are parallel to, but deeper than, the first pair. The second glabellar lobes are of similar length to the first pair but project beyond them so that the outline of the glabella is broken on either side by a " step " at the second glabellar furrows. The third glabellar furrows are deep and, near the axial furrows, almost parallel to the second glabellar furrows ; they then curve adaxially and sharply backwards, extending almost half the length of the third glabellar lobes. The three pairs of glabellar furrows terminate longitudinally in line, parallel to the median line. The third glabellar lobes are about one and a half times as long as the first and second glabellar lobes ; they are almost of " cat's ear " form and their abaxial margins are slightly indented. The axial furrows are broad and moderately shallow, becoming still shallower opposite the third glabellar lobes ; their rear halves are subparallel as far as the second furrows, in front of which, beyond the break in the glabellar outline described above, they become more strongly convergent forwards. The frontal glabellar lobe and the anterior portions of the fixigenae are bounded frontally by a broad (*sag.*), moderately-deep, transverse furrow, in front of which rises the anterior border, becoming thicker medially where its apex is bluntly pointed or gently rounded. The occipital furrow is narrow (*sag.*), moderately deep and transversely straight except for its median third where it becomes shallower and slightly convex forwards. The occipital ring is of almost uniform length (*sag.*), equal to about one-sixth that of the glabella, and carries a weakly-developed median node. The pleuroccipital furrow is broad (*exsag.*) and well defined, follows a gently sigmoidal course abaxially from the axial furrows and finally flexes more strongly towards its outer ends. The posterior border is of uniform breadth (*exsag.*) and runs parallel to the posterior border furrow as far as the rounded genal angles. The anterior portions of the fixigenae are equal to or rather more than half the corrresponding glabellar breadth ; the posterior portions contain well-developed paraglabellar areas which are semicircular in outline and abaxially convex, the breadth of each being about equal to one-quarter of the basal glabellar breadth. Each paraglabellar area is bounded adaxially by the axial furrow and abaxially by a semicircular furrow which meets the axial furrow frontally in a broad, pit-like depression opposite the third glabellar furrow. The palpebral lobes, though imperfectly known, are apparently crescentic in plan, moderately convex abaxially, extending backwards from points level with the first glabellar lobes as far as the line of the third glabellar furrows; their apices are level with the front half of the second glabellar lobes. They are defined adaxially by shallow palpebral furrows which extend from just outside the axial furrows, opposite the mid-points of the first glabellar lobes, until level with the middle of the paraglabellar areas ; the furrows then turn through slightly more than a right angle and extend rearwards until they intersect the paraglabellar areas ; the furrows then turn through slightly more than a right angle and extend backwards until they intersect the paraglabellar furrows. The anterior branches of the facial suture converge forwards parallel to the axial furrows as far as the anterior margin, where they turn adaxially and meet frontally. The posterior branches extend straight abaxially from the eyes almost half-way to the lateral margins, but then curve backwards through about 60 degrees and finally cut the lateral margins, apparently just in front of the rounded genal angles. The librigenae are not known with certainty, but a large specimen which probably belongs to the species is figured (Pl. 53, fig. 13). This is incompletely preserved but there is a suggestion of an eye-platform, outside of which the librigena is strongly convex and steeply declined towards the thickened border, from which it is separated by a broad, shallow, lateral border furrow.

The hypostoma and thorax are unknown.

The pygidium is tumid, wider than long in the ratio 5 : 3 or thereabouts, with rounded anterior and posterior margins which are strongly convex to front and rear respectively. Frontally the axis occupies about one-third of the maximum breadth of the pygidium, and extends almost to the tip of the latter. The axis is bounded laterally by deep, narrow, axial furrows which converge backwards strongly for about two thirds of their length and then become slightly less convergent as far as the tip ; there they join with a shallow but well-defined postaxial groove which separates the axis from the tip of the pygidium. Nearly all the available specimens have six axial rings, the sixth ring-furrow being shallow medially and obsolete distally. One small specimen (In. 54875) is exceptional in possessing seven axial rings, both the sixth and seventh ring furrows being obsolete distally. The terminal piece of the axis is swollen so as to produce a large, upwardly-directed, tubercle-like projection which is conspicuous even in a crushed specimen. In all the pygidia examined, each side-lobe has five ribs which diminish slightly in size from first to fifth and are separated from each other by deep, narrow (*exsag.*), pleural furrows. Each rib carries a faintly-impressed interpleural furrow which divides the rib into an anterior and a posterior band, the former being about twice as wide (*exsag.*) as the latter. The interpleural furrows are, for the most part, barely visible but each becomes suddenly and markedly deeper near the lateral margin which it intersects. The resulting notches, situated asymmetrically between adjacent pleural furrows, have the effect of producing a series of ten, tooth-like projections, alternately large and small in size, along either margin of the pygidium. There is sometimes a faint suggestion of a further pair of projections to the rear of the fifth pleural furrow.

With the exception of the furrows, the whole of the surface of the dorsal exoskeleton is covered by small, closely-grouped granules. These are particularly conspicuous on the outer surface of the test but less so on internal moulds.

HORIZONS AND LOCALITIES. The strata from which practically all the known specimens of *Platycoryphe dentata* have been collected form the *Harknessella subquadrata* Zone (known also as Beds or Limestone), the topmost subdivision of the Costonian Stage in the northern Caradoc Area. Only an occasional isolated specimen has been found in the succeeding Harnagian Stage of Coundmoor Brook (Pl. 55, fig. 3) ; this resembles the Costonian material in practically all respects but shows indications of eight axial rings, the seventh ring-furrow being obsolete distally and the eighth furrow still less well defined. The tip of this pygidium appears more prominent than usual owing to crushing which has emphasized the region immediately behind the axis. No specimens have been found in the Costonian of the southern Caradoc Area and only one individual, described later (p. 344) as *P.* cf. *dentata,* is known from rocks of, presumably, Harnagian age in the Horderley District.

Costonian localities include : the disused quarry in Black Dick's Coppice, Evenwood ; the section exposed in Bullhill Gutter, Evenwood ; disused quarries in the north-western and north-eastern parts of Round Nursery, south of Harnage Grange ; and the old quarry by the south-eastern side of Coundmoor Brook, 1,500 yards south-west of Harnage Farm, Harnage. The Harnagian locality, comprising shales of the *Reuscholithus reuschi* Zone, is in the south bank of Coundmoor Brook, 1,340 yards south-west of Harnage Farm.

HOLOTYPE. GSM. WM. 1335 (Pl. 53, fig. 1).

PARATYPES. GSM. WM. 1371 (Pl. 53, fig. 3) ; BM. In. 54875 (Pl. 53, figs. 2, 4) ; BM. In. 54876 (Pl. 53, fig. 5) ; GSM. WM. 1338 (Pl. 53, fig. 6).

OTHER FIGURED SPECIMENS. BM. In. 54584 (Pl. 53, fig. 7) ; BM. In 49310 (Pl. 53, fig. 9) ; BM. In. 54879 (Pl. 53, fig. 13) ; BM. In. 54913 (Pl. 53, fig. 3) ; BM. In. 54880 (Pl. 54, fig. 5) ; BM. In. 54325 (Pl. 55, fig. 3) ; GSM. 35516 (Pl. 55, fig. 10).

DISCUSSION. The manuscript name *Homalonotus biserratus* was applied by Reed (1918 : 273) to specimens, from the Hoar Edge Grits (of Costonian age) near Harnage, which had earlier been thought by Salter (1865*a*; pl. 10, fig. 13) to belong to *Homalonotus rudis*. The specific name used by Reed referred to the saw-like margins of the pygidium and he almost certainly had in mind the new species. He appears, however, to have used the name to include all the homalonotids of the Hoar Edge Grits and another specimen, a cranidium Sedgwick Mus. A. 43966 (Pl. 55, fig. 2), labelled by him as belonging to the same manuscript species is now known to be a typical *Brongniartella* and elsewhere in this paper is made one of the paratypes of *B. caradociana* sp. nov.

Platycoryphe dentata is close to the Czech species *P. bohemica* (Barrande, 1852: 580, pl. 34, figs. 40–42; 1872: 37, pl. 1, figs. 6, 7) from the Drabov Quartzites, of Llandeilo age. This species was re-examined by Prantl & Přibyl (1948: 7) and placed in *Eohomalonotus*. The figures of the Bohemian form suggest some variation in the proportions of the glabella, but none shows any trace of paraglabellar areas such as are strongly developed in the Shropshire species. The pygidium of *P. bohemica* bears a general resemblance to that of *P. dentata* and possesses a similar number of both axial rings (six or seven) and pleural ribs (five or six), the sixth and seventh axial rings becoming obsolete distally. The terminal piece of the pygidial axis in most figured examples of *P. bohemica* lacks the conspicuously tumid form found in the Shropshire species, though one specimen (Barrande, 1852, pl. 34, fig. 41) shows a weak development of this feature. The lateral margins of the pygidium are smooth, contrasting strongly with the serrated margins of *P. dentata*.

The type-species of *Platycoryphe* was first described by Foerste (1910: 81–82, pl. 2, fig. 7) as *Calymene platycephala* and was founded by him on a single cranidium. In many respects the latter resembles that of *P. dentata* but differs in having an " unstepped " glabellar outline, narrower fixigenae frontally, and a smaller, narrower (*tr.*), anterior border. There is a possible trace of a paraglabellar area on the right fixigena but the preservation of both fixigenae is too poor to be certain. A fragmentary pygidium tentatively assigned to *P. platycephala* (Foerste, 1910, pl. 4, fig. 21) has a narrower axis than that of *P. dentata*, with at least six axial rings. The pleural lobes have a larger number of ribs, six pairs, with a suggestion of a seventh pair; there is no trace of serrations along the lateral margins. The specimens of *P. platycephala* originated from the Saltillo Limestone of Tennessee, a horizon which Foerste (1910: 19) described as the stratal equivalent of the Hermitage Limestone, of middle Trenton age. The North American species is thus somewhat later in age than the south Shropshire specimens.

Platycoryphe dubia (Savage, 1913: 60, pl. 2, figs. 8, 9; Foerste, 1919: 395, pl. 19, figs. 15*a*, *b*) from the Girardeau Limestone (Richmondian) of Illinois differs markedly from all the above species. The axial furrows are uniformly convergent forwards, the basal glabellar lobes are smaller, bounded by straight third glabellar furrows, and paraglabellar areas are not developed. The front of the pygidium is only slightly convex forwards and the pleural furrows do not reach the margins. The species may only tentatively be retained in *Platycoryphe*.

Recently Whittard (1961: 164, pl. 22, figs. 8–19) has redescribed and figured *Platycoryphe vulcani* (Murchison) from the Weston Beds (high Llanvirn Series) of the Shelve Inlier, west Shropshire. This species is conspicuously different from

P. dentata, possessing a more trapezoidal glabellar outline with less well-developed glabellar furrows, and lacking paraglabellar areas and serrated pygidial margins. Some of the specimens figured by Whittard are difficult to distinguish from *Brongniartella*, and a reappraisal of the distribution of *Platycoryphe* in Britain must await the redescription of the type-species.

Two specimens are figured in this paper as *Platycoryphe* cf. *dentata* ; although they probably belong to that species, some doubt persists owing to the state of preservation.

Specimen BM. In. 51726 (Pl. 53, fig. 8) is a flattened, internal mould of an incomplete cranidium, the anterior border and palpebral lobes of which are missing. The glabellar outline is elongated and subtrapezoidal, and the axial furrows are almost straight. The second glabellar lobes are longitudinally in line with the first and third pairs of lobes and lack the distally projecting outline of those of *P. dentata*, but such modification might be the result of crushing. Despite the absence of the palpebral lobes the position of the eyes seems to be as in *P. dentata*, and the three pairs of glabellar furrows are of similar type, though somewhat distorted. BM. 51726 is from the Neptunian dyke in the north-eastern corner of the disused quarry on the south side of Hazler Hill, east of Church Stretton. The country rock forms part of the Eastern Uriconian (Pre-Cambrian) and the fissure infilling contains a fauna of early Harnagian age, equivalent to the zone of *Reuscholithus reuschi*, though the zonal trilobite has not been found there.

Cranidium GSM. 35524 (Pl. 53, fig. 10) was described by Salter (1865*a* : 108) as *Homalonotus edgelli*, but in the same work (pl. 10, fig. 10) he figured it as *Homalonotus bisulcatus*. Later, Reed (1918 : 272) considered the specimen to belong to the same group as *Homalonotus bisulcatus* and *H. ascriptus* Reed. In the shape of the narrow glabella and the medially thickened anterior border the specimen, a small internal mould, matches the narrow form of *Platycoryphe dentata*, but the glabellar furrows found in that species are completely absent. This may be due to the state of preservation and it seems unlikely that the specimen is specifically distinct. It is labelled merely as having been obtained from the " ? Caradoc " of " Horderley ", but the state of preservation is characteristic of the Smeathen Wood Beds which form an outcrop at and near the River Onny Valley, south-east of Horderley. These strata belong to both the *Reuscholithus reuschi* and *Salterolithus caractaci* Zones of the Harnagian Stage, but there is no indication as to which of these horizons provided the specimens.

Platycoryphe ? sp.

(Pl. 53, fig. 11 ; Pl. 55, fig. 14)

1958. *Eohomalonotus* sp. (? nov.), Dean, pp. 206, 221.

DESCRIPTION. Two isolated specimens which may belong to *Platycoryphe* have been collected from the Lower Longvillian rocks of the Onny Valley, strata much higher in the succession than any others in Shropshire known to contain the genus.

One, an incomplete cranidium (Pl. 53, fig. 11), is poorly preserved as an internal mould but can be seen to possess a glabella superficially similar to that of *Platycoryphe* *dentata*, though the frontal glabellar lobe is broader and more rectangular in outline. There are three pairs of straight glabellar furrows, directed adaxially and moderately rearwards from the axial furrows and becoming progressively deeper from first to third. They resemble those of *Platycoryphe dubia* (Savage) as figured by Foerste (1919, pl. 19, fig. 15*a*) and, like that species, the Longvillian form has smaller basal glabellar lobes than *P. dentata* and comparable forms. The anterior border is longer (*sag.*) and transversely straighter than that of *P. dentata* but the preservation is too poor to warrant a detailed comparison.

The other specimen, a small, convex pygidium (Pl. 55, fig. 14) is also somewhat indifferently preserved as an internal mould. The frontal margin is strongly arched forwards as in *Platycoryphe dentata*, and the axial furrows also become less convergent opposite the posterior third of the axis. There appear to be seven axial rings, the rearmost two of which are less well defined than the rest. The terminal piece is poorly preserved and a comparison with that of *P. dentata* is not possible. The pleural lobes possess at least five pairs of ribs, a number comparable with that found in *P. dentata*, but the pleural furrows are straighter and directed backwards even more strongly than in that species.

HORIZONS AND LOCALITIES. Cranidium BM. In. 50511 (Pl. 53, fig. 11) is from the middle third, the zone of *Dalmanella indica* and *D. lepta*, of the Lower Longvillian Substage exposed just west of the south-western corner of Rookery Wood, three-quarters of a mile south-east of Horderley.

Pygidium BM. In. 50816 is from the lowest third, the zone of *Dalmanella horderleyensis*, of the Lower Longvillian. The specimen was collected from the western end of the quarry by the north side of the Bishops Castle road, 250 yards south-east of Glenburrell Farm, Horderley.

Genus ***BRONGNIARTELLA*** Reed, 1918

TYPE SPECIES. *Homalonotus bisulcatus* M'Coy, 1851 *ex* Salter MS. by original designation of Reed (1918 : 322).

The authorshop of *Brongniartella bisulcata*, like that of *Kloucekia* (*Phacopidina*) *apiculata* (see p. 326) has usually been attributed to Salter though the species was, in fact, described first by M'Coy in 1851, Salter's description not being published until the following year. In M'Coy's original work (*in* Sedgwick & M'Coy, 1851, pl. 1G) figs. 24–29 were said to be *Homalonotus bisulcatus*, whilst figs. 30 and 31 were varieties of the species, but according to Salter (1852) figs. 29–31 were " variety *β minor* ", the specimens deriving from Bala and Westmorland.

Of the specimens figured by M'Coy, the original of his pl. 1G, fig. 24, was mistakenly stated, in the explanation of the plate, to have come from Pwllheli, though his text (p. 168) gave the locality correctly as " Wittingslow, near Acton Scott, Shropshire ". In the Appendix to M'Coy's work Salter stated that the originals of figs. 24, 26 and 27 came from Wittingslow (now Whittingslow, a farm three-quarters of a mile south-west of Marshbrook) and those of figs. 25 and 28 from Tremadoc (? Pwllheli). In attempting to clarify the species Reed (1918 : 270) stated erroneously that the originals of figs. 24, 26 and 27 were housed in the British Museum (Natural

History). In fact they are in the Geological Survey and Museum, though the counterpart of fig. 24 has now been traced in an old collection at the British Museum, where it is numbered In. 54914. Reed also stated, in my opinion correctly, that the species is undoubtedly established on Shropshire specimens and the original of M'Coy's fig. 24 is now chosen as lectotype. The present description is founded on the Shropshire syntypes, supplemented by further material from the type-area.

Brongniartella bisulcata (M'Coy)

Pl. 54, figs. 1, 2, 4, 8, 9; Pl. 55, figs. 1, 4, 7)

1847. *Homalonotus bisulcatus* MS., Sedgwick, p. 149. *Nomen nudum.*
1851. *Homalonotus bisulcatus* (Salter *in* Appendix), M'Coy *in* Sedgwick & M'Coy, p. 168.
1852. *Homalonotus bisulcatus* M'Coy: Salter, p. *v*.
1854. *Homalonotus bisulcatus* M'Coy: Salter *in* Morris, p. 109.
1859. *Homalonotus bisulcatus* M'Coy: Murchison, p. 74, fig. 2.
1865. *Homalonotus bisulcatus* M'Coy: Salter, pl. xvi, figs. 1–8.
1865*a*. *Homalonotus bisulcatus* M'Coy: Salter, p. 105, pl. 10, figs. 3, 4, 5, 9.
1867. *Homalonotus bisulcatus* M'Coy: Murchison, p. 69, fig. 2.
1884. *Homalonotus bisulcatus* M'Coy: La Touche, p. 57, pl. 3, fig. 62.
1918. *Homalonotus* (*Brongniartella*) *bisulcata* M'Coy: Reed, p. 322.
1930. *Homalonotus bisulcatus* M'Coy: Whitcomb, p. 348.
1947. *Brongniartella bisulcata* (M'Coy): Harper, p. 166.
1948. *Brongniartella bisulcata* (M'Coy): Prantl & Přibyl, p. 15.
1949. *Brongniartella bisulcata* (M'Coy): Bancroft, p. 309.
1958. *Brongniartella bisulcata* (M'Coy): Dean, pp. 207–210, 222–223.
1959*a*. *Brongniartella bisulcata* (M'Coy): Dean, pp. 207, 220.

DESCRIPTION. The cephalon is sub-semicircular in outline, blunted frontally. The glabella is trapezoidal in plan, gently convex both longitudinally and transversely, and stands slightly above the level of the remainder of the cephalon; it is slightly longer than broad, narrowing forwards slightly so that the breadth of the frontal lobe is about three-quarters of the basal breadth. The axial furrows are shallow with poorly-defined distal margins; for about half the length of the glabella they converge gently forwards from the occipital furrow, then suddenly converge more sharply, constricting the glabellar outline, and finally continue forwards parallel to their former course but set slightly closer together. Hypostomal pits are apparently absent. There are no glabellar furrows and the glabella is generally quite smooth though an occasional specimen, for example the lectotype, shows a suspicion of a low, longitudinal, median ridge. The anterior margin of the frontal glabellar lobe is weakly convex forwards, separated by an ill-defined furrow from the anterior border: the two last coalesce to form a broad (*sag.*), smooth, frontal brim which passes laterally without division into the anterior portions of the fixigenae. The occipital furrow is shallow but well defined, transversely straight for most of its length (*tr.*) but arched forwards medially, though this feature is less conspicuous in immature cranidia. The lectotype has part of the test preserved, showing that the occipital furrow is much less well defined on the external than on the internal surface. The occipital ring is of moderate, uniform length (*sag.*), generally about one-eighth that of the glabella; in plan it resembles a flattened trapezoid owing to the fact that the axial furrows diverge rearwards markedly on meeting the occipital furrow. The pleuroccipital furrow is set slightly to the rear of the occipital furrow; although shallow near the axial furrows it deepens abaxially at first but then becomes shallower again, at the same time curving gently forwards, and finally dies out without reaching the lateral margins. The posterior border, where it meets the axial furrows, is of the same length (*exsag.*) as the occipital ring, but becomes longer distally and terminates in bluntly-rounded genal angles. The fixigenae are large, each with a frontal breadth about, or rather less than, half that of the frontal glabellar lobe. Between the eyes and the sides of the glabella the fixigenae are level, but to the rear of the eyes they are turned down strongly, through about 70 degrees, towards the genal angles. The eyes are small, situated opposite the mid-point of the glabella, with small, smooth, palpebral lobes which are gently declined adaxially and pass without interruption into the fixigenae, palpebral furrows being absent. From the eyes the anterior branches of the facial suture extend forwards, roughly parallel, until opposite the front of the glabella, but then become more convergent, sweeping forwards and adaxially until they meet frontally, the suture so formed being above and just inside the naterior margin. The posterior branches of the facial suture run straight backwards from the eyes for only a short distance, then arch abaxially for about half their length, and finally curve back near the lateral margins which they cut acutely at, or immediately in front of, the genal angles. Only the more robust, triangular, hindmost portions of the librigenae are usually found. Each carries a broad, smooth, level eye-platform immediately beneath the visual surface of the eye, which has not been found preserved. Below each eye-platform the librigena is convex, steeply declined abaxially, and separated from the narrow, thickened lateral border by a shallow, broad, lateral border furrow which dies out towards the genal angle and so does not meet the pleuroccipital furrow.

The hypostoma has not previously been described or figured. The overall length and breadth are about equal, and the transverse convexity is greater than that longitudinally. The median body is moderately convex, slightly elongated, divided by a broad (*sag.*), shallow, median furrow into anterior and posterior lobes, the latter about one-quarter the length (*sag.*) of the former. The anterior border is narrow (*sag.*) medially, widening distally to form large anterior wings, the anterolateral margins of which are broad and obliquely truncated. The border is delimited by a broad (*sag.*), shallow furrow which curves backwards distally, meeting the median furrow, here slightly deeper, just behind the anterior wings. The lateral margins are deeply indented by large lateral notches which produce their maximum constriction of the outline almost opposite the mid-point of the hypostoma. Behind the lateral notches the lateral margins expand distally into rounded shoulders which form flanges directed ventrally at a moderate angle. The posterior margin of the hypostoma is forked, terminating in a pair of broad points separated by a deep, curved notch. Each point carries a small indentation, poorly preserved but perhaps representing a macula. The posterior border is separated from the posterior lobe of the median body by a broad (*exsag.*), shallow furrow which runs parallel to the median furrow, finally becoming deeper and terminating level with, and a short distance inside, the shoulders.

No complete thorax is yet known from south Shropshire, but one containing ten thoracic segments is figured here (Pl. 55, figs. 1, 4). The thoracic axis is broad, apparently more than twice the breadth of the side-lobes, though only slightly more than one-third of the total breadth in flattened specimens. Each axial ring is gently convex, its breadth (*tr.*) about eight to nine times the uniform length (*sag.*), and is separated from the articulating half-ring by a broad (*sag.*), shallow, articulating furrow. The axial furrow marking the distal end of each axial ring is oblique and runs abaxially from front to rear, its intersection with the posterior margin of the segment being marked by an articulating socket into which fits a corresponding articulating process on the subsequent segment. Outside the axial furrows the pleurae are of uniform breadth (*exsag.*), curving first slightly rearwards and then more strongly forwards to the large, bluntly-rounded tips. Each pleura carries a conspicuous pleural furrow which commences at the axial furrow as an abaxial continuation of the articulating furrow, and then arches gently back abaxially for almost half the length (*tr.*) of the pleura, when it becomes suddenly narrower (*exsag.*) and slot-like ; it then curves gently forwards towards the anterior margin and ends sharply without reaching either the margin or the pleural tip.

The pygidium is parabolic in outline, broader than long in the ratio of about 4 : 3, its anterior margin arched gently forwards. It is plump, convex both transversely and longitudinally, and the upper surface is moderately declined from front to rear. The axis is subtriangular in outline, bounded by smooth, shallow axial furrows ; frontally it occupies slightly less than half the maximum breadth, a proportion falling to a little less than one-third in flattened specimens. The number of axial rings ranges from nine to twelve, the most common number present being ten or eleven. The articulating furrow is deep but the remaining ring-furrows are less well defined and become fainter backwards ; they are not aligned with the rib-furrows of the side-lobes and do not quite attain the axial furrows. There are generally seven or eight ribs present on each side-lobe. The rib-furrows of the first pair are deep and narrow (*exsag.*) and those of the second pair are only slightly less strongly developed, but the remainder are markedly shallower. All these furrows become much attenuated at a narrow, poorly-defined border which they cross to reach the lateral margin. The border is best developed posterolaterally and at the tip of the pygidium where, in some specimens, it is turned up slightly to form a flange-like rim, though this feature may have been exaggerated by crushing.

HORIZONS AND LOCALITIES. *Brongniartella bisulcata* is one of the most abundant and characteristic of Shropshire trilobites and may be found at numerous localities along the Ordovician outcrop. It makes its appearance in the Alternata Limestone, the basal subdivision of the Upper Longvillian Substage, and it was from this horizon that the lectotype was originally collected. The species continues through the overlying Lower Cheney Longville Flags, the upper subdivision of the Upper Longvillian Substage, but it is in the succeeding Upper Cheney Longville Flags, representing the Marshbrookian Stage, that the greatest abundance is attained. No undoubted records from later strata are known, but rare fragmentary traces from the arenaceous development of the Actonian Stage suggests that the species may eventually prove to have persisted in south Shropshire after the close of the Marshbrookian in places where the environment was favourable.

LECTOTYPE. GSM. 7626 (Pl. 54, fig. 1). The counterpart of this specimen is in the British Museum (Nat. Hist.), where it is numbered In. 54914.

FIGURED SPECIMENS. BM. In. 48952 (Pl. 54, figs. 2, 4) ; BM. In. 50791 (Pl. 54, fig. 8) ; BM. In. 49557 (Pl. 54, fig. 9) ; GSM. 35519 (Pl. 55, figs. 1, 4) ; BM. In. 48598 (Pl. 55, fig. 7).

DISCUSSION. For convenience all the species of *Brongniartella* described in this paper will be discussed together at the end of the section.

Brongniartella caradociana sp. nov.

(Pl. 53, fig. 12 ; Pl. 54, figs. 3, 5, 7, 10 ; Pl. 55, fig. 2)

1918. *Homalonotus biserratus* Reed (*pars*), p. 273. MS. name only.
1958. *Brongniartella* aff. *bisulcata* (M'Coy) : Dean, p. 218.

DIAGNOSIS. Large species of *Brongniartella* distinguished by conspicuously broad glabella, narrowing frontally, large, scoop-like anterior border and broad fixigenae. Paraglabellar areas developed on immature individuals.

DESCRIPTION. The cephalon has not yet been found completely preserved. The cranidium is depressed, with median length about three-fifths of the maximum breadth. The glabella is gently convex, both longitudinally and transversely, its length equal to the basal breadth. The outline of the glabella in the adult trilobite is slightly more irregular than is usual for the genus. Shallow axial furrows, containing poorly-defined hypostomal pits frontally, run almost straight forwards for about half the length of the glabella, converging only very slightly ; they then become strongly convergent for a short distance, about one-seventh of the median length of the glabella, finally becoming less convergent as far as the anterolateral angles of the frontal glabellar lobe, the breadth of which is two-thirds that across the base of the glabella. In general there are no glabellar furrows present, but one specimen (Pl. 53, fig. 12) shows traces of shallow depressions which do not cut the axial furrows, but which meet mesially to form what appears as a single, broad (*sag.*), transglabellar depression or furrow. It is not clear whether this represents a pair of third glabellar furrows or whether it is the result of crushing. The frontal lobe of the glabella is slightly convex forwards, standing only slightly higher than the anterior border ; the latter is broad (*sag.*) and gently inclined anteriorly so that a slightly concave, scoop-like brim results, the frontal margin of which is arched forwards mesially. The distal portions of the occipital furrow are deep and transversely straight but the median third is markedly shallower and, in the largest-known specimen, convex forwards, though straight in small individuals. The occipital ring is of almost uniform length (*exsag.*) which increases slightly mesially. In small individuals the lines of the axial furrows diverge rearwards from the frontal edge of the occipital furrow, cutting the outer ends of the occipital ring obliquely. The occipital ring of the holotype, a large and presumably mature specimen, passes abaxially into the posterior border, only faint traces of axial furrows being present. The posterior border furrow is transversely straight, moderately deep, and is set slightly to the rear of the occipital furrow. The posterior border is not yet completely known, but the inner parts, at least, are transversely straight and of uniform breadth (*exsag.*). The genal angles have not yet been found intact. The fixigenae are large and conspicuously broad ; frontally their individual breadth equals more than half that of the frontal glabellar lobe in the holotype, a proportion rising to more than two-thirds in smaller specimens. The hindmost portions of the fixigenae of immature specimens carry conspicuous, slightly-raised, subcircular, paraglabellar areas, each defined posteriorly and adaxially by the posterior border furrow and axial furrow respectively, and frontally and abaxially by a continuous, shallow, arched furrow. In smaller individuals the paraglabellar areas indent the axial furrows which then appear slightly concave abaxially, but in the largest specimen they are scarcely visible. The eyes are small, situated forwards of centre of the glabella. Small palpebral lobes are continuous with the upper surface of the fixigenae and gently declined adaxially ; no palpebral furrows have been seen. The anterior branches of the facial suture arch forwards and adaxially from the eyes, meeting the anterior border in line with points mid-way between the palpebral lobes and the frontal glabellar lobe, and then converge frontally. The posterior branches curve abaxially backwards from the eyes to the as yet unknown genal angles.

The librigenae and hypostoma are unknown.

Only one specimen of the thorax has been discovered, a poorly-preserved individual (Pl. 54, fig. 3) with twelve, or possibly thirteen, segments. The thoracic axis is broad, occupying about half the total breadth. Each axial ring is of uniform length (*sag.*), bounded distally by shallow axial furrows which converge forwards markedly. Each pleura is of fairly uniform breadth (*exsag.*) and directed slightly rearwards abaxially ; it carries a pronounced pleural furrow which commences at the line of the axial furrow, almost cutting the frontal margin, and then runs distally and gently backwards finally pursuing an almost median course towards the tip. It is not clear from the available material whether the furrow actually reaches the tip, nor is the shape of the latter known.

A single pygidium, small and possibly immature, which may probably be referred to the new species has been collected. Though incompletely preserved, it is broader than long, approximately in the ratio 9 : 7, and semielliptical in outline. The axis occupies more than one-third of the frontal breadth, is moderately tapered towards the bluntly-rounded tip, and occupies about nine-tenths of the overall length, excluding the articulating half-ring. Seven axial rings are visible, becoming less well defined posteriorly, but they extend for only three-quarters of the length of the axis. The pleural lobes carry five pairs of ribs, defined by pleural furrows which appear to extend to the lateral margins. The first axial ring furrow is deep and cuts the straight, moderately-deep, axial furrows in line with the equally deep first pair of pleural furrows. The remaining axial ring furrows do not quite intersect the axial furrows and are not in line with the corresponding pleural furrows. The second pleural furrows are slightly shallower than the first, and the remaining pleural furrows become progressively shallower.

The surface of the test in all the materal available is covered with fine pitting visible only under the microscope.

Horizon and localities. All the known specimens of *Brongniartella caradociana* are from the limestones and calcareous sandstones forming the upper portion of the Costonian Stage, the zone of *Harknessella subquadrata*, in the district around Evenwood and Harnage Grange, near the northern end of the outcrop of the Caradoc Series in the type-area. Important localities are: the old quarry by the south-eastern side of the brook, 1,500 yards south-west of Harnage Farm; the section in Bullhill Gutter, Evenwood; various old quarries in Round Nursery, south-south-east of Harnage Grange; and Black Dick's Quarry, Evenwood.

HOLOTYPE. BM. In. 51485 (Pl. 53, fig. 12).

PARATYPES. BM. In. 50769 (Pl. 54, fig. 10); BM. In. 54871 (Pl. 54, fig. 7); BM. In 54880 (Pl. 54, fig. 5); BM. In. 54913 (Pl. 54, fig. 3). Sedgwick Museum A. 43866 (Pl. 55, fig. 2).

Brongniartella minor (Salter)

(Pl. 54, fig. 6; Pl. 55, fig. 11)

1851. *Homalonotus bisulcatus* (Salter *in* Appendix), M'Coy *in* Sedgwick & M'Coy, p. 168 (*pars*), pl. 1G, fig. 30 (? also fig. 29).
1852. *Homalonotus bisulcatus* var. β *minor*, Salter, p. v.
1873. *Homalonotus bisulcatus* M'Coy: Salter, p. 53.
1891. *Homalonotus bisulcatus* M'Coy: Woods, p. 145.
1918. *Homalonotus bisulcatus* M'Coy var. β *minor* Salter, Reed, p. 270.
1947. *Brongniartella parva* Harper, p. 165, pl. 6, figs. 7, 8.

Several specimens were described and figured by M'Coy (*in* Sedgwick & M'Coy, 1851: 168, pl. 1G, figs. 24–31) as *Homalonotus bisulcatus*. Of them the original of fig. 29 was unlocalized, whilst the originals of figs. 30 and 31 were stated in the text to be " supposed varieties " from " Ravenstone Dale ", although in the explanation of the plate the latter locality was modified to " Ravenstone Dale, Maes Meillion ". In his supplement to the foregoing work Salter (1852: v) applied the name *Homalonotus bisulcatus* var. *β minor* to the originals of figs. 29–31, both 29 and 30 being stated to derive from Bala and 31 from Westmorland. Mr. A. G. Brighton kindly informs me that the original of fig. 29 cannot now be traced in the Sedgwick Museum, and has made available the other syntypes, numbered A. 10574 (fig. 30) and A. 10576 (fig. 31).

A. 10574, which may be referred to the genus *Brongniartella*, is a pygidium said to be from the " Bala Limestone " of Maes Meillion, near Bala, Merioneth. It is associated, on the same hand-specimen, with *Kloucekia apiculata* (M'Coy), *Flexicalymene* cf. *caractaci* (Salter), *Sampo* sp. (? *oepiki* Whittington) and ? *Paucicrura sowerbii* Cave & Dean; the specimen is therefore probably of Lower Longvillian age. Owing to the state of preservation of the surface of the type pygidium it is not easy to determine the exact number of axial rings and pleural ribs present, but there appear to be eight and seven respectively. These numbers are the same as those described by Harper (1947: 166) for *Brongniartella parva*, a species which possesses a similar pygidial outline and was described from the Lower Longvillian strata of Ynys Galed, Caernarvonshire. Pygidium A. 10574 is selected here as the lectotype of *Brongniartella minor*, of which species *Brongniartella parva* Harper is now regarded as a subjective synonym.

The other syntype of *Homalonotus bisulcatus* var. *β minor* is a pygidium numbered A. 10576. The locality, given as " Ravenstone Dale ", together with the state of preservation, suggests that it was obtained from the Upper Ordovician strata of the Cautley district in north-west Yorkshire, between Sedbergh, Yorkshire, and Ravenstonedale, Westmorland. *Homalonotus sedgwicki* was described from the same neighbourhood by Salter (1865*a* : 107) and founded by him on cranidia only ; the species is in need of revision but may prove to be conspecific with the specimen figured by M'Coy. Should this be the case, the name *Homalonotus sedgwicki* would be available for both specimens.

In south Shropshire a few cranidia have been collected which agree in size and proportions with the holotype of *Brongniartella parva* Harper. All the specimens are preserved as internal moulds found in weathered lenses of sandy limestone within the Horderley Sandstone ; they are apparently undistorted and show no trace of the median ridge found in *B. minor subcarinata* subsp. nov. (see later), a form which possibly also occurs, though rarely, in the Horderley Sandstone.

HORIZONS AND LOCALITIES. The earliest-known specimen is from the Lower Horderley Sandstone, Upper Soudleyan Stage, zone of *Broeggerolithus soudleyensis*, at the small, disused, road-side quarry 100 yards south-east of Glenburrell Farm, Horderley. The youngest specimen was obtained from the topmost beds of the Horderley Sandstone, the *Bancroftina typa* Zone of the Lower Longvillian Substage, at the disused quarry by the west side of New House, Horderley. Harper's type material of *Brongniartella parva* was collected from North Welsh strata containing *Dalmanella indica* Whittington together with other typical Lower Longvillian species.

FIGURED SPECIMENS. BM. In. 52315 (Pl. 54, fig. 6) ; BM. In. 51529 (Pl. 55, fig. 11).

Brongniartella minor subcarinata subsp. nov.

(Pl. 55, figs. 6, 8, ? 13)

1958. *Brongniartella* sp., Dean, pp. 203, 220.
1961. *Brongniartella* aff. *minor* (Salter) : Dean & Dineley, p. 374, pl. 20, figs. 3, 7.

DIAGNOSIS. Subspecies of *Brongniartella minor* characterized by presence of median ridge on glabella, and constriction of glabella outline frontally. Pygidium with seven axial rings and five pleural ribs.

DESCRIPTION. Several specimens have been found, particularly in the Lower Soudleyan strata of south Shropshire, of a *Brongniartella* showing an obvious resemblance to *B. minor* (Salter) but differing consistently from that species in a few respects. There is generally a slight constriction of the glabellar outline at about its mid-point, a feature seen also in *Brongniartella bisulcata* and *B. caradociana* (see earlier) ; its apparent absence from the North Welsh specimens may, however, be due to their being mechanically deformed and is probably not of major significance. The obvious difference in the glabella of the Shropshire subspecies is the presence of a pronounced longitudinal ridge coincident with the sagittal line over the median half of the glabellar length. Such a structure has not been observed in *Brongniartella minor*, perhaps owing to deformation ; on the other hand, Shropshire cranidia figured in this paper as *Brongniartella minor* are apparently undistorted but show no sign of a median carina.

The pygidium of the new subspecies is of generally similar outline to that of *B. minor*, but the number of axial rings and pleural ribs is consistently smaller, being respectively seven and five, compared with eight and seven.

HORIZON AND LOCALITIES. The new subspecies has been found in moderate abundance in the higher Glenburrell Beds, representing the Lower Soudleyan Stage, zone of *Broeggerolithus broeggeri*. Localities include : the stream-section at the extreme north-eastern corner of Smeathen Wood, Horderley ; the exposure behind the farmhouse, Glenburrell Farm, Horderley ; and the cartway 50 yards north-east of Glenburrell Farm.

A further specimen referred tentatively to the same subspecies (Pl. 55, fig. 13) was collected from the Horderley Sandstone, Lower Longvillian Substage, zone of *Dalmanella indica* and *D. lepta*, at the old quarry by the west side of the path through Longville Plantation, 720 yards north-west of the "Earthwork" at Cheney Longville. No stratigraphically intermediate specimens have yet been found, and this suggests that the subspecies may have been subject to ecological control, showing a preference for the mudstone environment of the Glenburrell Beds rather than the, presumably, shallower conditions which gave rise to the Horderley Sandstone. The same subspecies has been collected from Habberley Brook, north-west of The Longmynd, where the higher beds of the so-called Pontesford Shales have a lithology and fauna similar to that of the Lower Soudleyan of the Onny Valley.

HOLOTYPE. BM. In. 50781 (Pl. 55, fig. 6).

PARATYPE. BM. In. 51182 (Pl. 55, fig. 8).

OTHER SPECIMEN?. BM. In. 51726 (Pl. 55, fig. 13).

Brongniartella edgelli (Salter)

(Pl. 55, figs. 9, 12)

1865*a*. *Homalonotus edgelli* Salter, p. 108, pl. 10, fig. 11 only.
1918. *Homalonotus edgelli* Salter : Reed, p. 270.

The type and only known specimen is an incomplete, damaged pygidium, preserved as an internal mould, having an estimated projected length of 9 mm. and a frontal breadth of about 11 mm. It is strongly convex transversely and highest frontally, its dorsal surface moderately declined rearwards. The anterior margin is convex forwards medially, and terminates laterally in a pair of large facets. The lateral margins are relatively straight for the genus and converge from the anterolateral facets at roughly 60 degrees. The tip of the pygidium is missing but the border there appears to have possessed a small lateral flange. The narrow pygidial axis occupies about one-third of the frontal breadth and tapers gently backwards, delimited laterally by deep, straight, axial furrows. The surface of the axis is damaged but, excluding the articulating half-ring, there are five axial rings in just over half the length. The side-lobes are convex, narrowing backwards and declined steeply towards the lateral margins ; each has a well-developed facet and carries seven pleural furrows, the first two of which are deep, the others becoming shallower and extending almost as far as the tip of the axis. All the pleural furrows are well defined as far as the inner margin of the doublure, but can scarcely be traced to the lateral margins owing to the poor state of preservation.

HORIZON AND LOCALITY. The specimen is a limonitic internal mould embedded in a fragment of green-brown, fine-grained sandstone. The matrix is somewhat indeterminate, but is suggestive of that found in the Lower Cheney Longville Flags. The label states merely " Acton Scott ", but as this name was often used in old collections to denote the whole of the Acton Scott-Marshbrook district it is of little value. A reliable appraisal of the stratigraphical position of *Brongniartella edgelli* must therefore await the collection of further material.

HOLOTYPE. GSM. 35525.

Brongniartella sp.

(Pl. 55, fig. 5)

One specimen has been collected, an incomplete pygidium, which is apparently distinct from the other forms of *Brongniartella* in south Shropshire and may represent a new species. The pygidium, preserved as an internal mould, is almost semicircular in outline, only moderately convex, with median length about two-thirds of the maximum breadth. The axis, occupying just over three-quarters of the median length and, frontally, rather more than one-third of the maximum breadth, tapers sharply rearwards. Laterally it is defined by straight, shallow, axial furrows, and it passes into the border with no development of a postaxial ridge. Excluding the articulating half-ring there are seven axial rings, extending almost to the tip of the axis. Each pleural lobe is moderately declined abaxially, with traces of up to seven ribs. There is evidence of small anterolateral facets and although the first two pleural furrows are deep the remainder become rapidly shallower, with the hindmost barely visible ; they end abaxially at a narrow border which becomes broader (*sag.*) at and near the tip of the pygidium.

HORIZON AND LOCALITY. The pygidium was collected from a lenticular bed of weathered, sandy limestone occurring in massive sandstones of the Horderley Sandstone at the south-eastern corner of Rookery Wood, three-quarters of a mile south-east of Horderley. The horizon is in the Lower Longvillian Substage, zone of *Dalmanella indica* and *D. lepta*.

FIGURED SPECIMEN. BM. In. 51520.

DISCUSSION. *Brongniartella caradociana* is of particular interest as it is the earliest species of the genus known from south Shropshire, appearing suddenly in the topmost Costonian strata within a geographically restricted area of the county. The holotype is also the largest form of *Brongniartella* yet known in the Caradoc District prior to *B. bisulcata*, which does not appear until much later, at the base of the Upper Longvillian Substage. All the stratigraphically intervening species are of small size. Our incomplete knowledge of the pygidium *B. caradociana* makes comparison with other species difficult, but the cephalon is easily distinguished from that of *B. bisulcata* by the broad glabella and large size of the fixigenae. Small individuals provisionally assigned to *B. caradociana* possess distinctive paraglabellar areas which have not yet been seen in any of the other Shropshire material of *Brongniartella*. The name *Homalonotus rudis* has sometimes been applied to specimens of *Brongniartella* now known to belong to *B. caradociana*. *H. rudis* was first described and figured by M'Coy (*in* Sedgwick & M'Coy, 1851 : 168, pl. 1E, figs. 20, 20*a*) from the Capel Garmon district, Denbighshire, and the syntypes are in the Sedgwick Museum, where they are numbered A. 10564 and A. 10565. Both are incomplete, distorted pygidia from which it is virtually impossible to obtain an accurate impression of the species, and it is suggested that the specific name should no longer be used until well-preserved topotype material has been adequately figured and described.

The eastern North American species *Brongniartella trentonensis* (Simpson) has been shown by Whitcomb (1930) to be remarkably similar to *B. bisulcata*, but the glabella of the former is narrower and conspicuously more carinate than that of the latter, whilst the pygidium of *B. trentonensis*, although possessing a comparable number of axial rings and pleural ribs, is proportionately broader and has an axis which is more strongly convergent posteriorly.

The characteristic species of the genus during the Lower Longvillian is *B. minor*, a form which may have developed from the closely similar *B. minor subcarinata*. The latter may be separated on the basis of the carinate glabella and the smaller number of axial rings and pleural ribs, and its presence in the Lower Longvillian is somewhat doubtful ; it is certainly more characteristic of the Lower Soudleyan and has not yet been found coexisting with *B. minor*.

The relationship between the generally small species of *Brongniartella* existing in south Shropshire during the deposition of the Soudleyan and Lower Longvillian rocks, and the large *B. bisulcata* of the Upper Longvillian is still not clear. Certain other shelly fossils, for example *Kloucekia* and *Bancroftina*, exhibit a trend towards a larger size of individual above the boundary separating Lower and Upper Longvillian in south Shropshire, perhaps as the result of a change in environment, but such an explanation seems inadequate to explain the appearance of *B. bisulcata*, and it is more likely that the latter is an immigrant form, perhaps from elsewhere in the Anglo-Welsh area.

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EXPLANATION OF PLATES

Specimen numbers with prefixes BM. In., GSM. and A. are housed respectively in the British Museum (Natural History), London, the Geological Survey & Museum, London, and the Sedgwick Museum, Cambridge. All specimens were whitened with ammonium chloride before being photographed.

PLATE 49

Acanthoparypha stubblefieldi (Bancroft) . . . . p. 314

Harnagian Stage, zone of *Reuscholithus reuschi*, section in old cartway near southern end of Smeathen Wood, Horderley.

Figs. 1, 4. Incomplete, undistorted cranidium preserved as internal mould, showing outline and convexity of glabella. BM. In. 50499. ×2·1.

Fig. 3. Paratype, internal mould of pygidium. BM. In. 42085. ×2.

Figs. 5, 11. Lectotype, internal mould of incomplete, slightly distorted cranidium. BM. In. 42084. ×2·25.

Fig. 6. Internal mould of fragment of glabella showing true outline posterolaterally. BM. In. 50498. ×2·25.

Pseudosphaerexochus sp. . . . . . . p. 316

Onnian Stage, zone of *Onnia superba*, north bank of River Onny, 720 yards west-south-west of Wistanstow Church.

Figs. 2, 7, 8. Almost complete distorted cephalon preserved as internal mould. BM. In. 50660. ×2.

Kloucekia (*Phacopidina*) *harnagensis* (Bancroft) . . . p. 321

Horizon and locality as for Fig. 1.

Figs. 9, 14. Latex cast from almost complete external mould of dorsal exoskeleton, showing thoracic segments, pygidium, and upturned terminal spine. BM. In. 49131. ×1·5.

Encrinurus sp. (? nov.) . . . . . . p. 317

Marshbrookian Stage, zone of *Dalmanella unguis*, Marshwood Quarry, ½ mile south of Marshbrook Station.

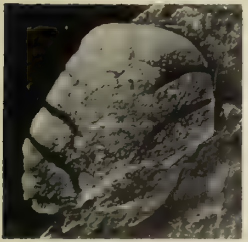
Figs. 10, 12. Internal mould of pygidium. BM. In. 49312. ×2·5.

Atractopyge sp. . . . . p. 318

Middle Actonian Stage, disused quarry by east side of road, opposite Church Farm, Acton Scott.

Fig. 13. Latex cast from external mould. BM. In. 49319. ×2.

Figs. 3, 9, 10, 12–14, by Mr. J. Brown, remainder by the writer.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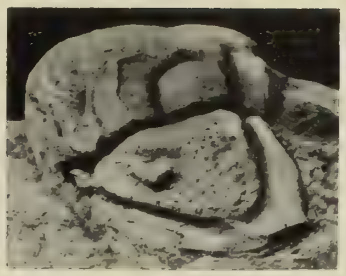
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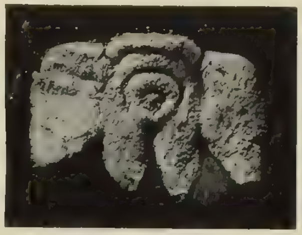
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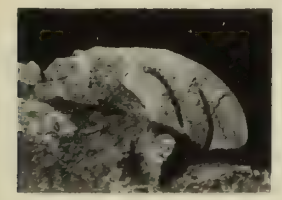
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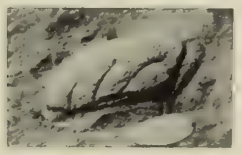
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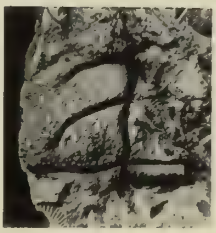
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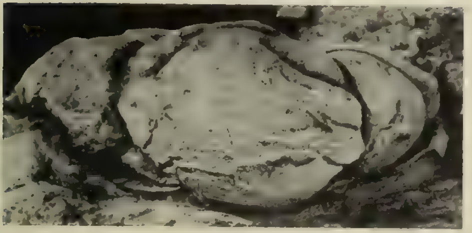
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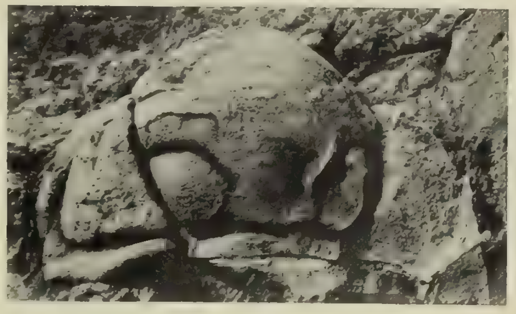
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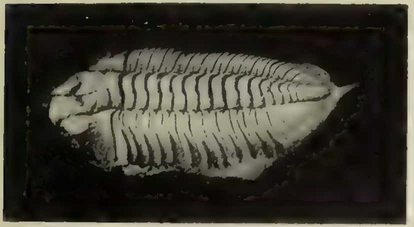
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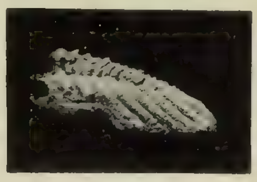
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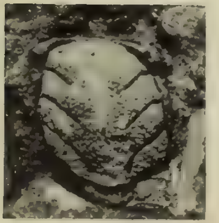
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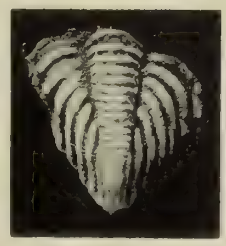
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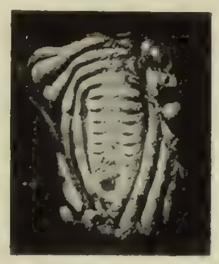
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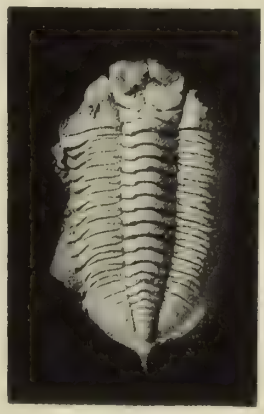
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ACANTHOPARYPHA, ATRACTOPYGE, ENCRINURUS,
KLOUCEKIA (PHACOPIDINA), PSEUDOSPHAEREXOCHUS

PLATE 50

Kloucekia (*Phacopidina*) *harnagensis* (Bancroft) . . . p. 321

Harnagian Stage, zone of *Reuscholithus reuschi*, section in old cartway near southern end of Smeathen Wood, Horderley.

FIGS. 1, 5. Lectotype B.M. In. 42089. ×2·3.

FIG. 2. Cranidium showing visual surface of eye. BM. In. 50576. ×4.

FIG. 3. Paratype pygidium. BM. 42088. ×3·5.

FIG. 4. Internal mould of immature cranidium, showing deep first and second glabellar furrows. BM. In. 52211. ×5.

Kloucekia (*Phacopidina*) *apiculata* (M'Coy) . . . p. 324

Upper Longvillian Substage, zone of *Kjaerina bipartita*. Soudley Quarry, by Soudley Pool, near Hope Bowdler.

FIGS. 6, 10. Internal mould of cephalon showing palpebral furrow and fixigenal spine. BM. In. 54864. ×2.

FIG. 12. Internal mould of whole individual with terminal spine preserved. BM. In. 50558. ×1·5.

Horizon as for Fig. 6. Bed of stream by west side of Horderley/Marshbrook road, 560 yards north-east of Crosspipes.

FIGS 7, 8. Pygidium showing upturned terminal spine. BM. In. 51259. ×2·2.

FIG. 9. Latex cast from external mould of cephalon showing glabellar furrows and palpebral lobe. BM. In. 51260. ×3·3.

Calyptaulax actonensis sp. nov. . . . . . p. 328

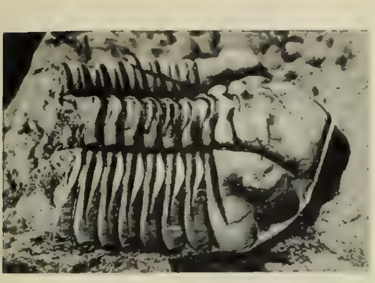
Middle Actonian Stage, site of old quarry, Quarry Field, Gretton, near Cardington.

FIGS. 11, 14. Holotype pygidium, an internal mould. BM. 49771. 11, ×2; 14, ×2·5

Horizon as for Fig. 11. Probably from the north side of the Bishops Castle road, south-west of Wistanstow.

FIG. 13. Internal mould of pygidium. BM. In. 48492. ×2·2.

Figs. 2, 12, 14, by Mr. E. W. Seaville, remainder by the writer.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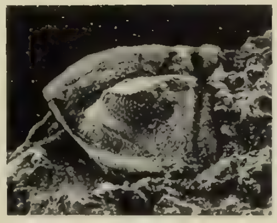
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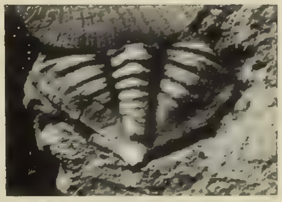
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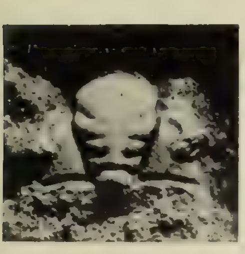
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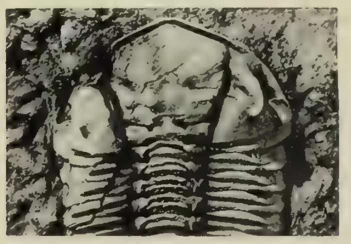
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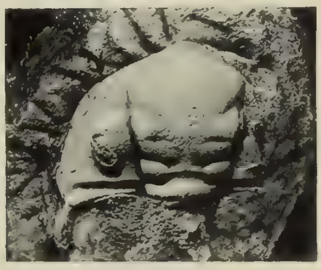
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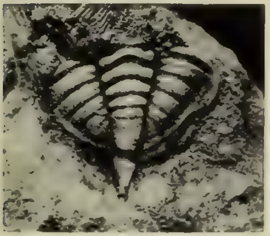
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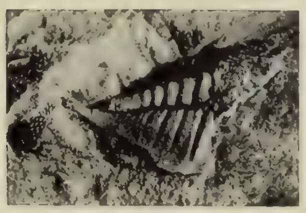
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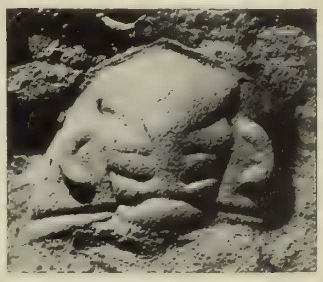
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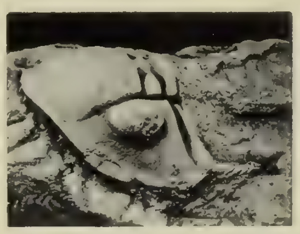
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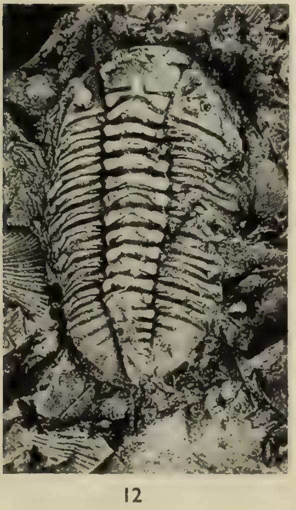
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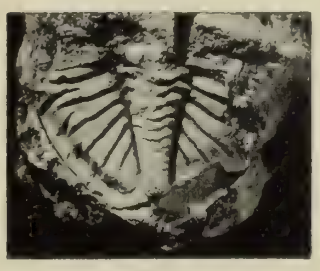
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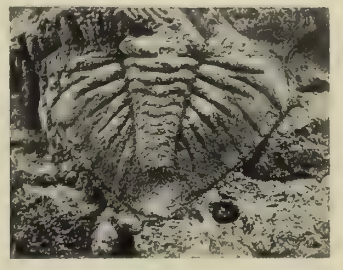
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CALYPTAULAX, KLOUCEKIA (PHACOPIDINA)

PLATE 51

Calyptaulax actonensis sp. nov. . . . . . p. 328

Middle Actonian Stage, site of old quarry, Quarry Field, Gretton, near Cardington.

FIG. 1. Paratype cranidium, an internal mould. BM. In. 49318. ×2·3.

FIG. 2. Latex cast from external mould of incomplete paratype cranidium. BM. In. 49768. ×3.

Chasmops extensa (Boeck) . . . . . . p. 331

Upper Longvillian Substage, zone of *Kjaerina typa*, old quarry below path at north-eastern corner of Burrells Coppice, south-east of Horderley.

FIG. 3. Internal mould of incomplete cranidium. BM. In. 50547. ×1·4.

FIG. 7. Internal mould of pygidium. BM. In. 50546. ×1·1.

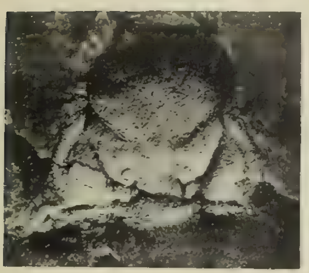
Middle Actonian Stage, south bank of River Onny, 80 yards west of junction with Batch Gutter.

FIGS. 4, 8, 10. Almost complete large cephalon with part of test preserved. BM. In. 49127. ×1.

FIGS. 5, 9. Pygidium with test preserved. BM. In. 49128. ×1.

FIG. 6. Hypostoma preserved as internal mould. BM. In. 49126. ×1.

Figs. 2, 3 and 7 by Mr. E. W. Seavill, remainder by Mr. J. Brown.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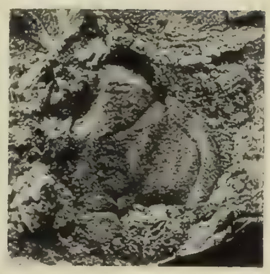
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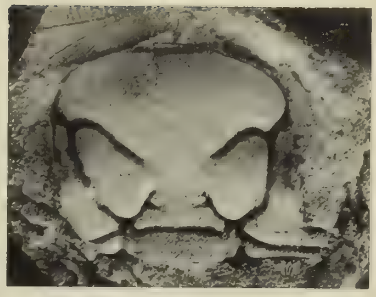
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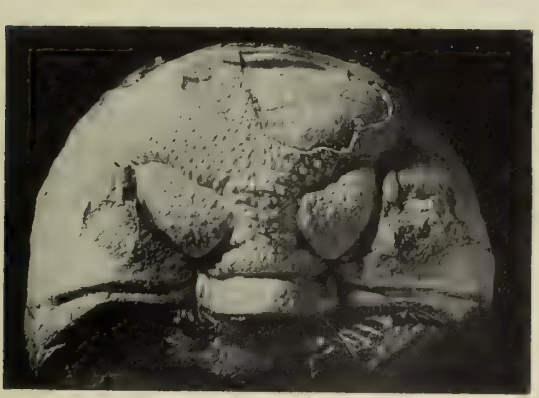
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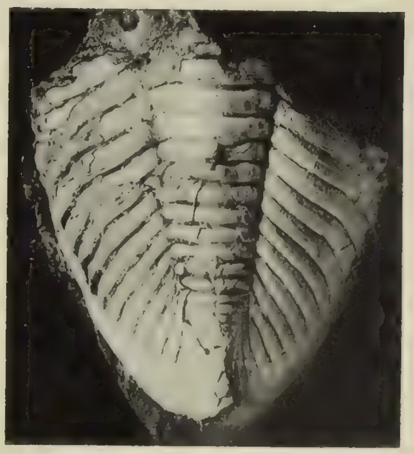
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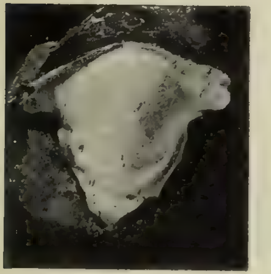
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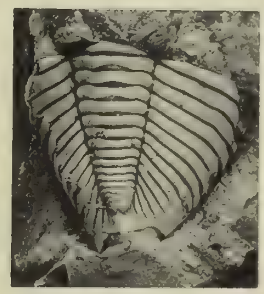
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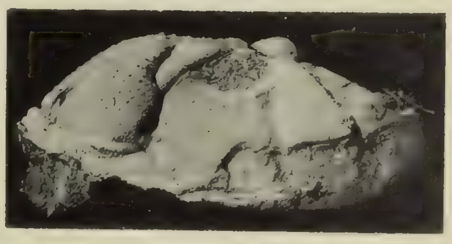
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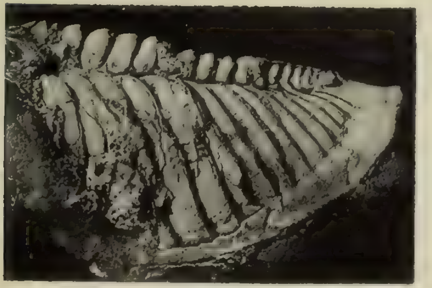
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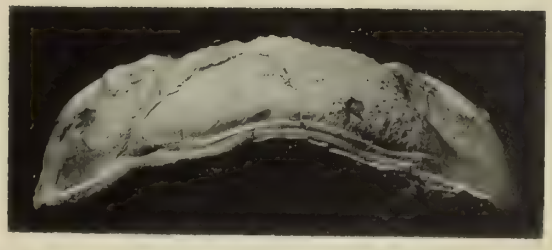
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CALYPTAULAX, CHASMOPS

PLATE 52

Chasmops extensa (Boeck) . . . . . . p. 331

Marshbrookian Stage, zone of *Onniella reuschi*, road-fork 75 yards north-north-east of Woolston House, Woolston.

Fig. 4. Incomplete cranidium. BM. In. 50548. × 2.

Middle Actonian Stage, south bank of River Onny 80 yards west of junction with Batch Gutter.

Fig. 1. Enlargement to show surface of glabella near frontal rim. BM. In. 49127. × 5.

Fig. 6. Surface of glabellar lobes showing constitution of the large tubercles. BM. In. 49127. × 6.

Fig. 7. Enlargement to show surface granulation of pygidium. BM. In. 49128. × 5·5.

Onnian Stage, zone of *Onnia ? cobboldi*, south bank of River Onny 45 yards east of junction with Batch Gutter.

Fig. 3. Incomplete cranidium. BM. In. 50549. × 1·8.

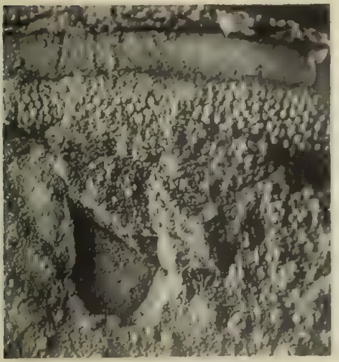
Chasmops salopiensis sp. nov. . . . . . p. 337

Uppermost Actonian Stage, north bank of River Onny 30 yards east of junction with Batch Gutter.

Fig. 2. Internal mould of pygidium tentatively assigned to the species. BM. In. 50552. × 2.

Fig. 5. Holotype, an incomplete cephalon with test partially preserved. BM. In. 50551. × 2.

Figs. 1, 6 and 7 by Mr. J. Brown, 2 and 5 by Mr. E. W. Seavill, 3 and 4 by the writer.



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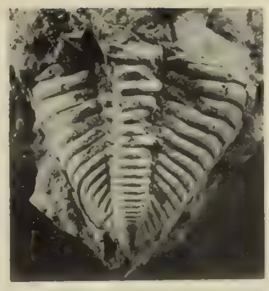

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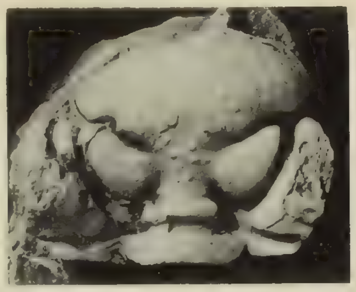

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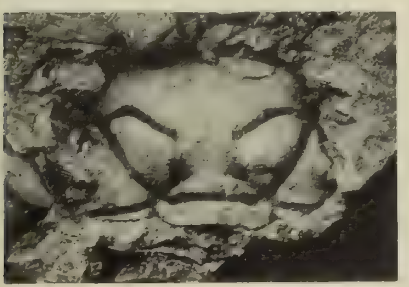

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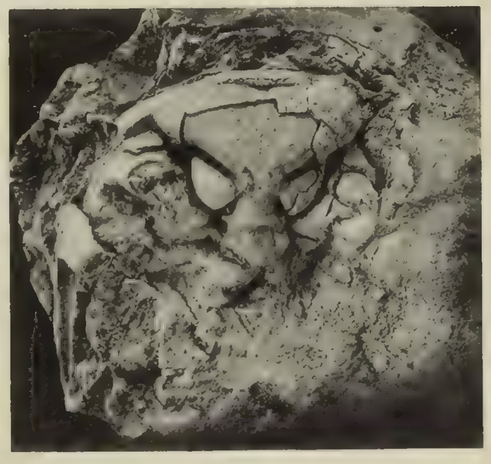

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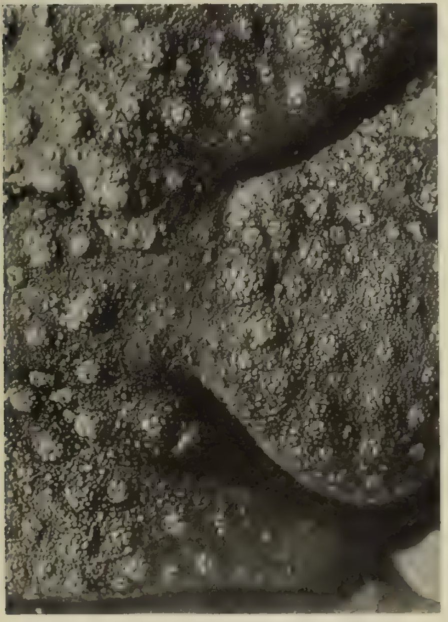

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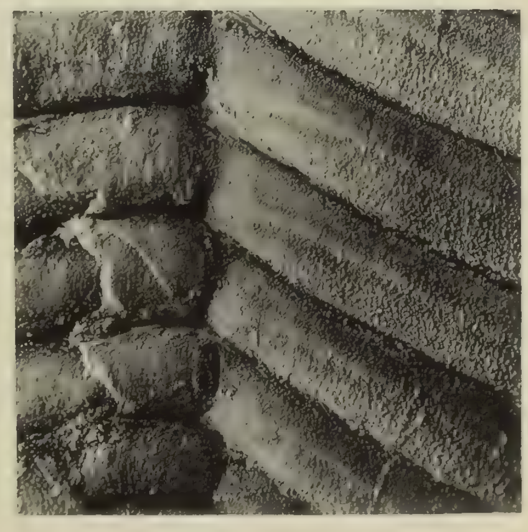


7

CHASMOPS

PLATE 53

Platycoryphe dentata sp. nov. . . . . . p. 340

Costonian Stage, *Harknessella subquadrata* Beds, old quarry near eastern end of Black Dick's Coppice, Evenwood.

FIG. 1. Holotype cranidium. GSM. WM 1335. ×1·5.

FIG. 3. Paratype cranidium. GSM. WM 1371. ×2.

FIG. 6. Paratype pygidium. GSM. WM 1338. ×2.

Horizon as for Fig. 1. Small quarry in north-western part of Round Nursery, south of Harnage Grange.

FIGS. 2, 4. Paratype pygidium illustrating swollen terminal piece of the axis. BM. In. 54875. ×2·8.

FIG. 5. Large paratype cranidium showing paraglabellar areas. BM. In. 54876. ×2·2.

FIG. 7. Pygidium preserved as flattened external mould. BM. In. 54874. ×2·2.

FIG. 13. Librigena preserved as internal mould. BM. In. 54879. ×1·8.

Horizon as for Fig. 1. Old quarry by south-eastern side of brook, 1,500 yards south-west of Harnage Farm, Harnage.

FIG. 9. Internal mould of incomplete cranidium with narrow form of glabella. BM. In. 49310. ×1·5.

Platycoryphe cf. *dentata* sp. nov. . . . . p. 344

Harnagian Stage, zone of *Reuscholithus reuschi*, neptunian dyke in eastern corner of quarry on south side of Hazler Hill, east of Church Stretton.

FIG. 8. Internal mould of incomplete cranidium. BM. In. 51726. ×2·2.

Horizon probably as for Fig. 8. Locality shown only as " Horderley ", but see p. 344.

FIG. 10. Internal mould of small cranidium, figured by Salter (1865, pl. 10, fig. 10) as *Homalonotus bisulcatus*, but referred by him in the same paper (p. 108) to ? *Homalonotus edgelli*. GSM. 35524. ×3·4.

Platycoryphe? sp. . . . . . . p. 344

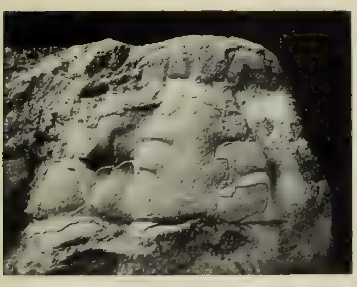
Lower Longvillian Substage, zone of *Dalmanella indica* and *D. lepta*. Exposure west of south-western corner of Rookery Wood, south-east of Horderley.

FIG. 11. Incomplete cranidium preserved as internal mould in decalcified sandstone. BM. In. 50511. ×2.

Brongniartella caradociana sp. nov. . . . . . p. 349

Horizon and locality as for Fig. 9.

FIG. 12. Holotype cranidium preserved as an internal mould. BM. In. 51485. ×1·75.
Photographs 1, 3, 6 and 9 by Mr. J. Brown ; remainder by the writer.



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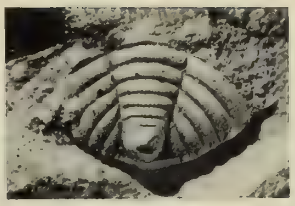

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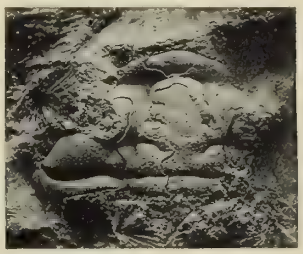

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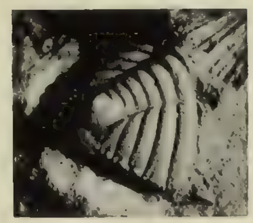

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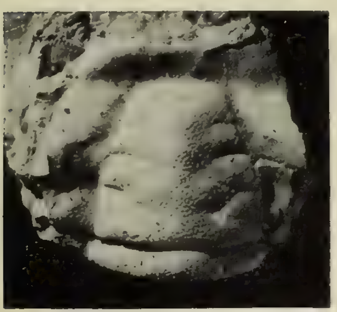

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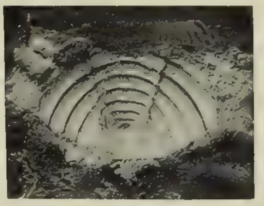

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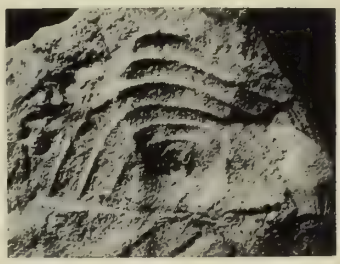

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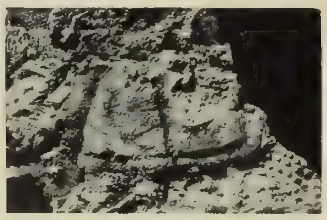

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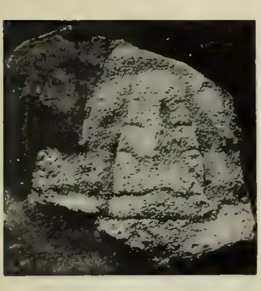

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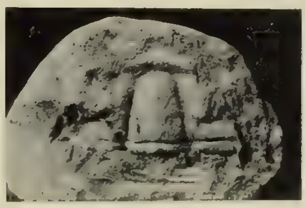

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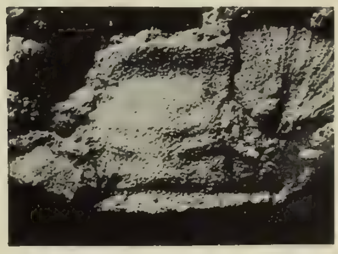

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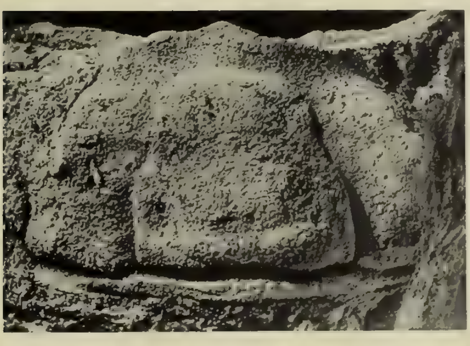

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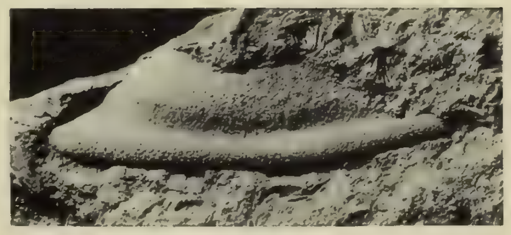

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BRONGNIARTELLA, PLATYCORYPHE

PLATE 54

Brongniartella bisulcata (M'Coy) . . . . . p. 346

Upper Longvillian Substage, zone of *Kjaerina bipartita* (=Alternata Limestone). Localized merely as " Whittingslow ", south of Marshbrook.

FIG. 1. Lectotype cranidium with part of test preserved. GSM. 7626 (counterpart = BM. In. 54914). ×1·5.

Marshbrookian Stage, zone unknown, Marshbrook.

FIGS. 2, 4. Cephalon with librigenae in position. BM. In. 48592. ×1.

Marshbrookian Stage, zone of *Dalmanella wattsi*, Marshwood Quarry, ½ mile south of Marshbrook Station.

FIG. 8. Flattened cranidium showing exaggerated tape of glabellar outline. BM. In. 50791. ×1·1.

Horizon as for Fig. 1. Soudley Quarry, near Soudley Pool, south-east of Hope Bowdler.

FIG. 9. Internal mould of almost complete hypostoma. BM. In. 49557. ×1·8.

Brongniartella caradociana sp. nov. . . . . . p. 349

Costonian Stage, *Harknessella subquadrata* Beds, section in Bullhill Gutter, Evenwood.

FIG. 3. Latex cast from external mould of incomplete thorax. BM. In. 54913. ×2·4.

Horizon as for Fig. 3. Old quarry in north-western part of Round Nursery, south-south-east of Harnage Grange.

FIG. 5. Internal mould of incomplete thoracic segment. BM. In. 54880. ×2.

Horizon and locality as for Fig. 5.

FIG. 7. Latex cast from external mould of paratype pygidium. BM. In. 54871. ×4.

Horizon as for Fig. 3. Old quarry in Black Dick's Coppice, Evenwood.

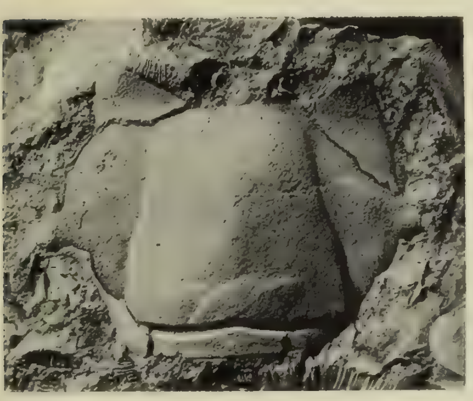
FIG. 10. Incomplete paratype cranidium with part of test intact, showing paraglabellar areas. BM. In. 50769. ×3.

Brongniartella minor (Salter) . . . . . p. 351

Lower Longvillian Substage, zone of *Bancroftina typa*, old quarry by west side of New House, south-east of Horderley.

FIG. 6. Incomplete cranidium preserved as internal mould in decalcified sandstone. BM. In. 52315. ×1·8.

Photographs by the writer.



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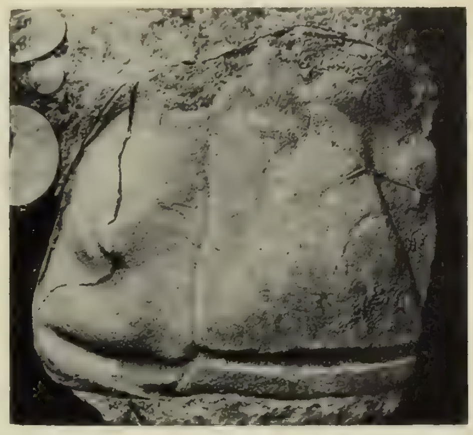

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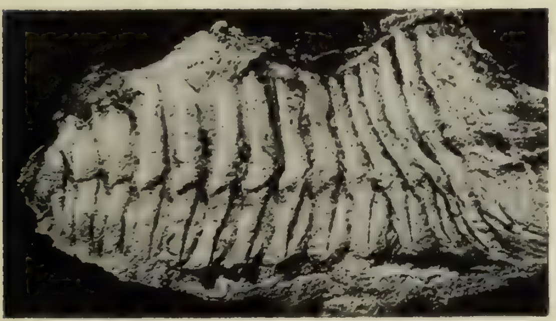

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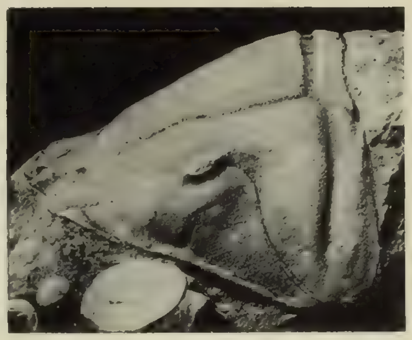

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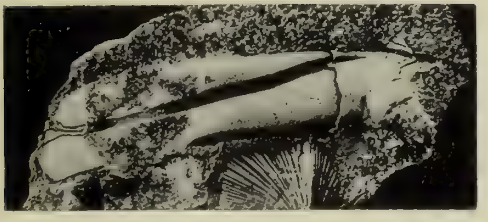

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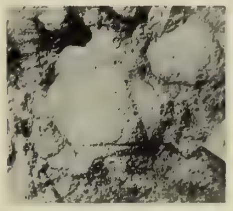

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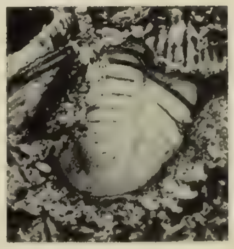

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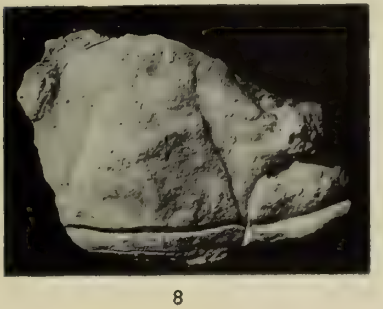

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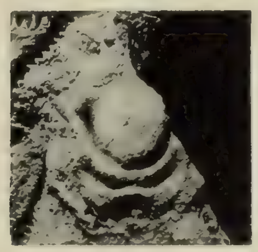

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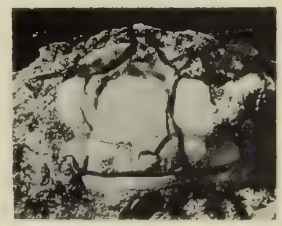

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BRONGNIARTELLA

PLATE 55

Brongniartella bisulcata (M'Coy) . . . . . p. 346

Marshbrookian Stage, localized only as " Marshbrook ".

Figs. 1, 4. Pygidium with ten attached thoracic segments. GSM. 35519. ×2.

Horizon as for Fig. 1. " Near Horderley."

Fig. 7. Internal mould of pygidium. BM. In. 48598. ×1·1.

Brongniartella caradociana sp. nov. . . . . . p. 349

Costonian Stage, probably zone of *Harknessella subquadrata*, " near Harnage Grange ".

Fig. 2. Incomplete paratype cranidium with part of test preserved. Sedg. Mus. A. 43866. ×1·5.

Platycoryphe dentata sp. nov. . . . . . p. 340

Harnagian Stage, zone of *Reuscholithus reuschi*, south bank of Coundmoor Brook, 1,340 yards south-west of Harnage Farm, Harnage.

Fig. 3. Depressed pygidium with part of granulated test preserved, but dentate margin absent. BM. In. 54235. ×3·4.

Horizon and locality probably as for Fig. 2.

Fig. 10. Latex cast from external mould of incomplete pygidium, GSM. 35526. The internal mould of the same specimen, GSM. 35527, was figured by Salter (1865, pl. 10, fig. 13 ; 1865*a*, pl. 16, fig. 11) as ? *Homalonotus rudis*. ×1.

Brongniartella sp. . . . . . . p. 354

Lower Longvillian Substage, zone of *Dalmanella indica* and *D. lepta*, south-eastern corner of Rookery Wood, south-east of Horderley.

Fig. 5. Nearly complete pygidium preserved as internal mould. BM. In. 51520. ×1·8.

Brongniartella minor subcarinata subsp. nov. . . . . p. 352

Soudleyan Stage, zone of *Broeggerolithus broeggeri*, stream-section at north-eastern corner of Smeathen Wood, Horderley.

Fig. 6. Holotype, almost complete cranidium preserved as internal mould. BM. In. 50781. ×2·5.

Horizon as for Fig. 6. Section behind north-western corner of Glenburrell Farm, Horderley.

Fig. 8. Internal mould of pygidium. BM. In. 51182. ×2.

Horizon as for Fig. 5. Small quarry by west side of path through Longville Plantation, *c.* 60 yards from north-eastern corner.

Fig. 13 ?. Small, incomplete pygidium, preserved as internal mould and only tentatively referred to the subspecies. BM. In. 51726. ×2·5.

Brongniartella edgelli (Salter) . . . . . p. 353

Localized merely as " Acton Scott ", but probably from the Cheney Longville Flags of the Marshbrook district.

Figs. 9, 12. Holotype pygidium, an internal mould. GSM. 35525. ×2·5.

Brongniartella minor (Salter) . . . . . p. 351

Soudleyan Stage, zone of *Broeggerolithus soudleyensis*, quarry by north side of road 100 yards south-east of Glenburrell Farm, Horderley.

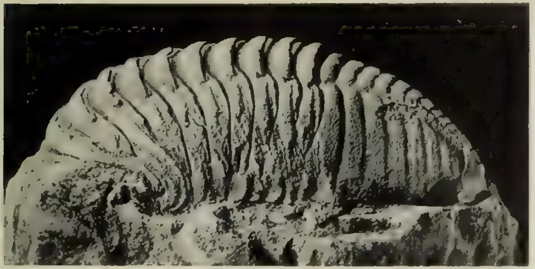
Fig. 11. Internal mould of incomplete cranidium. BM. In. 51529. ×2.

Platycoryphe? sp. . . . . . . p. 344

Lower Longvillian Substage, zone of *Dalmanella horderleyensis*, west end of quarry by north side of road, 250 yards south-east of Glenburrell Farm, Horderley.

Fig. 14. Internal mould of complete pygidium. BM. In. 50816. ×2·5.

Fig. 2 by Mr. J. Brown, Fig. 6 by Mr. E. W. Seavill, remainder by the writer.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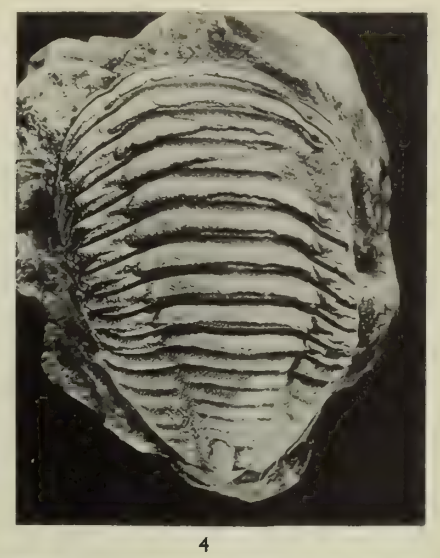
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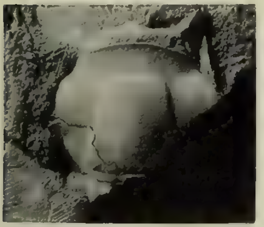
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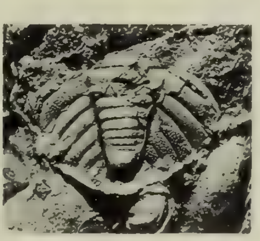
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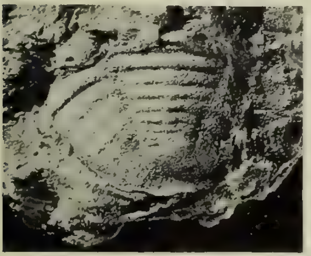
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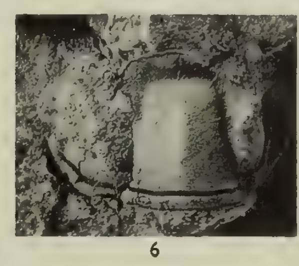
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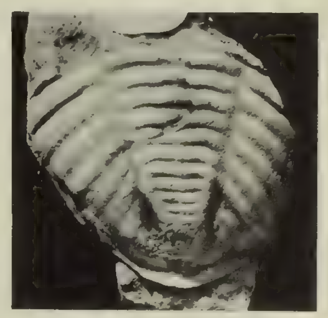
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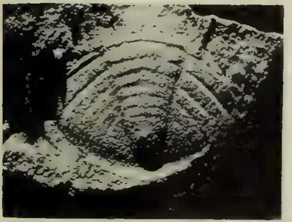
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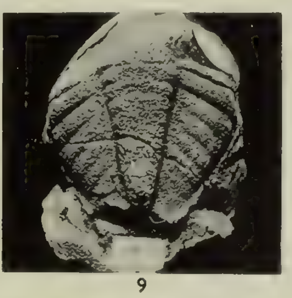
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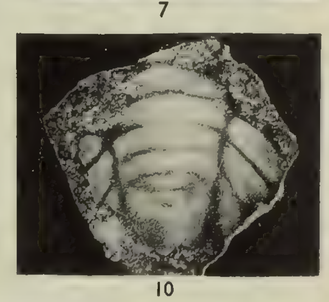
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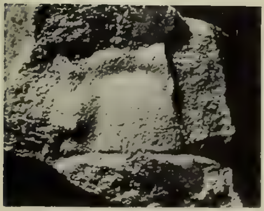
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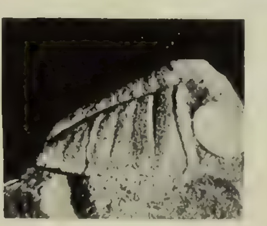
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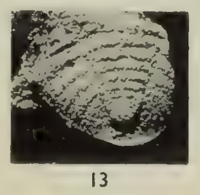
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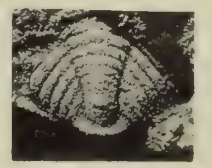
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BRONGNIARTELLA, PLATYCORYPHE

THE MORPHOLOGY OF *BOTRYOPTERIS ANTIQUA*

BRITISH MUSEUM
19 APR 62
NATURAL HISTORY

H. S. HOLDEN

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 5 No. 9
LONDON: 1962

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BY

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Pp. 359–380 ; *Plates* 56–60 ; 12 *Text-figures*

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THE MORPHOLOGY OF *BOTRYOPTERIS ANTIQUA* KIDSTON

By HENRY SMITH HOLDEN

SYNOPSIS

An account is given of the morphology of *Botryopteris antiqua*, a small fern from the Lower Carboniferous. It discusses the work of previous investigators and re-interprets this in the light of the discovery of additional material. The species is diagnosed and a lectotype chosen.

INTRODUCTION

In 1908 the late Robert Kidston published a relatively short description of a minute fossil fern from the Lower Carboniferous of Burntisland, Fifeshire, which he named *Botryopteris antiqua*. Although his account of the morphology of this plant was, in some respects, incomplete it provided adequate data for its ready recognition by subsequent investigators. Petioles from the Culm of Autun, France, closely resembling those described by Kidston had been known for some time and specimens from this locality were investigated by Pelourde (1910) who, in his paper, states that Kidston regarded the French specimens as being conspecific with those described by him. This view has been generally accepted (Bertrand, 1912 ; Scott, 1920 ; Corsin, 1937) although we have no adequate knowledge of the stems to which the Autun petioles belonged. It is a point of interest in this connection that, whilst with very rare exceptions, the petioles from Burntisland are oval in transverse section those from Autun that have been studied by the author consistently show a well-marked adaxial concavity (Pl. 60, fig. 4) a characteristic also recorded in the specimens from Autun examined by Corsin (1937 : 223, 225). This difference is one of the criteria used in the specific separation of the Cheilanthoid ferns and it suggests the possibility that the French specimens may well belong to a different, though closely allied, species.

Among the more important characters established by Kidston was the fact that the xylem of the stem stele consisted entirely of tracheids without any admixture of parenchyma. He was unable, however, to distinguish in the stem any groups of protoxylem. He also described the main features of the petiole and leaf trace. In the latter he interpreted as protoxylem a band of small tracheids with scalariform thickening normally occupying the more pointed adaxial side of the trace but in some examples, such as that in his fig. 8, forming a narrow band down both sides of the metaxylem and even extending to the abaxial margin. The thickenings of the tracheids of the petiolar metaxylem he described as porose. He also figured a specimen (figs. 11, 12) which he interpreted as being an example of petiolar dichotomy.

Three years after the publication of Kidston's paper Margaret Benson, who had obtained further specimens from Burntisland, gave a fuller description of the plant and, among other things, suggested a different interpretation of some of the sections figured by Kidston (Benson, 1911). Benson's material enabled her to trace the connection between the vascular supply of the petiole and that of the stem and to show that the protoxylem in the petiole was initially mesarch in position. She regarded the plant as " heterophyllous " and considered that the stem bore petioles of two kinds. One of these, which she termed the monarch type, had a single adaxial protoxylem group and was accompanied by a uninerved sheathing organ which she interpreted " as of the nature of an aphlebia ". The second type of lateral structure arising from the stem, which she regarded as a diarch petiole, possessed two adaxial protoxylem groups and was not accompanied by an aphlebia-like structure. She stated that the protoxylem in both types of petiole became " aggregated into one or two adaxial grooves " and that the diarch traces appeared to be preceded and followed by monarch ones. The smaller elements and protoxylem according to her show all intermediate types of thickening from porose to reticulate.

The sections studied by both Kidston and Benson were prepared by grinding down thin slices of the rock containing the fossil until they were transparent enough to be examined by transmitted light. The drawback to sections prepared in this way, especially in dealing with incomplete and frequently fragmentary specimens, is that it is often impossible to be certain of the exact relationships between the separate parts such as stem and petiole and even to be certain that they belong to the same plant. With the advent of modern " peel " techniques some of these difficulties have disappeared and the most recent investigation of *Botryopteris antiqua* by Surange (1952) using such techniques has added materially to our knowledge of the plant. He has established the fact that the tip of the young petiole was circinately coiled (Pl. 59, fig. 3) and has suggested a new interpretation of the morphology differing radically from that put forward by Benson.

Surange interprets the structures termed diarch petioles by Benson as dorsiventral stems from which radial stems, possessing an abundant system of adventitious roots, arise and on which true petioles (i.e. Benson's monarch petioles) are developed in spiral succession. The development of a radially organized stem from the diarch axis is initiated by the separation from it of a lateral trace. This is smaller than the parent axis and carries with it one of the two protoxylem groups. The radial stem, which is characterized by the smaller calibre of its tracheids, develops on the adaxial side of the branch near its base and is adnate to it. Surange states that, in the material examined by him, the structure he terms a dorsiventral stem " invariably gives rise to a radial stem and to no other structure ". He also states that the tracheids of the petiolar protoxylem show spiral thickenings.

Prior to the publication of Surange's paper a number of specimens of *Botryopteris antiqua* from Burntisland had been collected with the intention of making a fuller study of its morphology but, in view of the differing interpretations resulting from the work of the previous investigators to which reference has already been made, it was considered desirable to examine also the sections upon which they had based their views. For this purpose Professor Walton, Head of the Botany Department of Glasgow University, kindly loaned to the Museum not only the slides figured by Kidston but also the whole of the slides of *Botryopteris antiqua* in the Kidston Collection. In addition to these he also loaned slides containing sections of the petiole of *B. antiqua* from the departmental Figured Slide Collection which he had collected from a locality in Dunbartonshire. Professor Jane, of the Royal Holloway College, was equally helpful with regard to the slides of *Botryopteris antiqua* from the Benson Collection as was Dr. Hamshaw Thomas with regard to those studied by Surange. The grateful thanks of the author are due to all these fellow botanists for their ready co-operation. In addition to the Kidston, Benson and Surange slides several from the Gordon Collection were kindly looked out and sent over to the Museum by Dr. O. Bradley of the Department of Geology, King's College, London, and Mr. A. G. Long sent me his sections of the specimen of *B. antiqua* to which reference is made in Surange's paper.

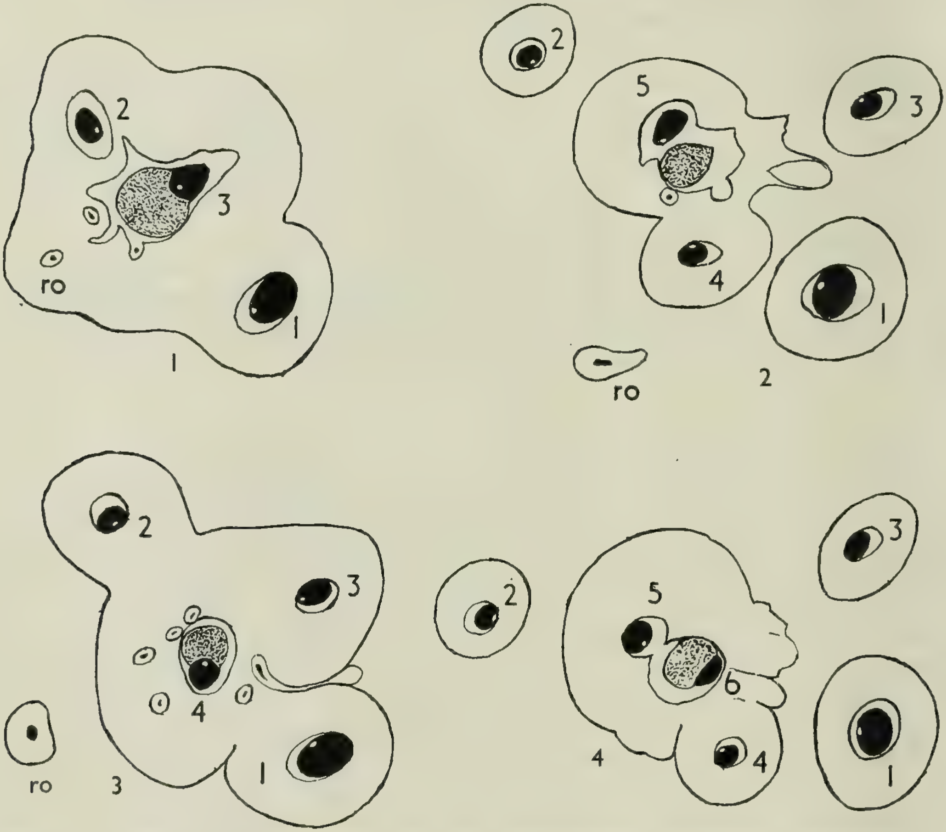
These slides together with those in the Oliver and Scott Collections and that of the author form the basis of the present account but, in addition, a large number of " peels " have been made from blocks of Lower Carboniferous material from that part of the Hemingway Collection which is now in the British Museum (Natural History), Department of Palaeontology. The majority of these " peels " have been prepared by C. H. Shute, Scientific Assistant in the Department.

The study of the considerable number of specimens indicated above, whilst it has not provided an answer to all the morphological problems raised by this Lower Carboniferous fern, has enabled a fuller and more detailed account of its morphology to be given than had been possible previously.

DESCRIPTION

The Stem

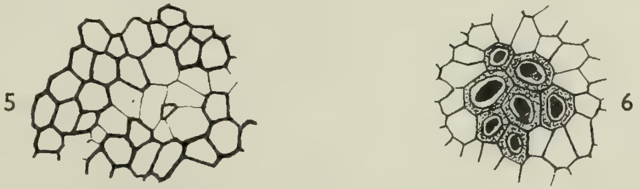
A typical plant of *Botryopteris antiqua* possesses a radially organized stem developing abundant adventitious roots. These roots are most numerous at and near the base of the stem but are also produced quite close to the apex (e.g. Pl. 56, figs. 1, 3). The stem bears closely set spirally arranged petioles which, in many specimens, show a two-fifths divergence (Pl. 56, fig. 1 ; Text-figs. 1–4) though this is by no means constant. Its centre is occupied by a stele which has the shape of a shallow dome. The stelar xylem is composed entirely of tracheids which are smaller in diameter than those of the petioles (Pl. 56, fig. 1) and which show predominantly scalariform pitting though this type of pitting may be replaced by a reticulate type with transversely elongated pits at and near the periphery. Near the stem apex where the differentiation of the tracheids is not completed thin-walled cells occur scattered among the xylem elements which are already lignified (Pl. 59, fig. 6 ; Text-fig. 5). The protoxylem occupies a mesarch position and consists of single minute tracheids or groups of these distributed near the outer part of the stele. The determination of the nature of the protoxylem thickenings proved to be a matter of some difficulty but its spiral character is clearly shown in one of Surange's slides (B 78) and is illustrated in Pl. 58, figs. 1, 2. Neither the phloem and its associated parenchyma nor the inner cortex are preserved in most specimens so that there is a gap between the stelar xylem and the tissues forming the middle and outer cortex (Pl. 56, fig. 1 ; Text-figs. 1–4). There are a few sections, however, in which some or all of these tissues are present and two of these from the Gordon Collection are illustrated in Pl. 56, fig. 2 and Pl. 57, fig. 1. In these sections there are indications that the phloem consisted of a more or less continuous ring of large sieve tubes and phloem parenchyma similar to that occurring in *Ankyropteris corrugata* and many other Palaeozoic ferns. The bulk of the inner cortex is composed of small-celled parenchyma but, scattered among this, there are a number of groups of thick-walled cells with dark contracted contents (Text-fig. 6). The middle cortex consists of larger, somewhat thick-walled, cells many of which, like the similar groups in the inner cortex, possess dark contents (Pl. 56, fig. 2). These thick-walled cells merge into a well-defined parenchymatous outer cortex of cells larger than those of the inner cortex enclosed by the small-celled epidermis. The surface of the stem, especially at and near the apex, bears numerous hairs. These are pointed and predominantly uniseriate though occasionally they possess a stouter multicellular base (Text-figs. 7*a*–*g*). They are present also on the basal parts of the petioles but do not appear to extend on to the more distal parts of



FIGS. 1–4. Camera lucida drawings of four transverse sections showing a two-fifths spiral sequence of monarch petiole traces. Figs. 1–3 show three stages in the emission of a reduced lateral outgrowth (*ro*). The petiolar bundles are numbered in the order of their development. All × 15. B.M. (N.H.) Holden Coll., slides H.92, H.153, H.177, H.192.

these. The actual stem apex is roofed in by a closely set mantle of these hairs which acted, presumably, as a protective cover for the delicate underlying tissues.

Two specimens of the stem in which the stele shows an equal dichotomy have been noted. The better example of this condition is that shown in Slide No. 549*c* and figured by Kidston (1908, fig. 6).



FIGS. 5, 6. Fig. 5, Transverse section of part of the stem stele near its apex showing the incompletely differentiated metaxylem and an isolated mesarch protoxylem tracheid. B.M. (N.H.) Oliver Coll. 1247. × 80. Fig. 6, A small group of dark sclerized cells from the inner cortex of the stem. Gordon Coll., King's College. × 80.

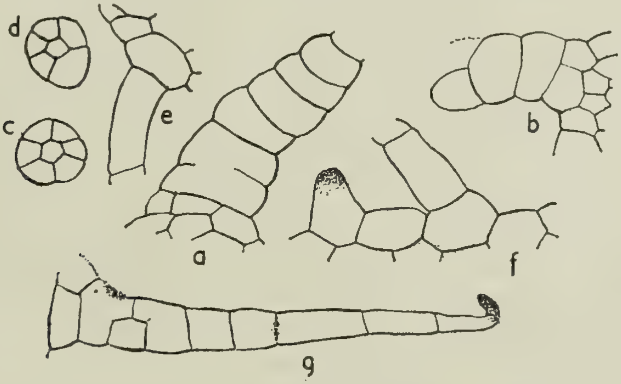


FIG. 7. Hairs from the stem and the base of the petiole. *a–d*, Kidston Coll., Glasgow University, slide 549*c*; *e–g*, Hemingway Coll., B.M. (N.H.) No. V.35555 (sections 35, 52 and 98 respectively). All × 135 approx.

The Petiole

As has been stated already, the petioles arise from the stems in a close spiral and usually show an approximately two-fifths divergence (Text-figs. 1–4). In the great majority of specimens the xylem and cortex are the only tissues preserved and even these may show some degree of breakdown. In the case of the xylem the protoxylem is the only part affected but the cortical tissues may become disorganized and, partly or almost wholly, be replaced by aggregates of calcite. These have crushed and ruptured the cortical cells and produced a pseudo-cellular structure in which the sphaerules of calcite have become surrounded by the broken down cell remnants (Pl. 57, fig. 6). This condition is not uncommon in petrified plant remains from Burntisland and was noted and figured by Gordon in some of the specimens of *Diplolabis* examined by him (Gordon, 1911).

The protoxylem of the petiole trace is initially mesarch with a single protoxylem group situated close to the adaxial surface. This mesarch position of the protoxylem persists for a short time after the separation of the trace from the stem stele but endarchy is usually attained by the time the petiole is free from the stem. The petiole trace is ovoid in transverse section with the spirally thickened protoxylem tracheids forming a distinct adaxial ridge (Pl. 56, fig. 1). Quite commonly, however, the protoxylem tracheids show partial or more or less complete disintegration and either are not preserved at all or are represented by dissociated fragments of the spiral thickening. An example of this latter condition is shown in Pl. 58, fig. 1, from a longitudinal section in the Figured Slide Collection of the Botany Department, Glasgow University. It is this variation in the degree of preservation of the protoxylem which probably accounts for the differing descriptions of Kidston (1908), Benson (1911) and Surange (1952). It seems evident that the small tracheids described by Kidston as protoxylem are in fact metaxylem elements and that the median groove described by Benson as situated in the centre of the protoxylem group is due to the loss of the spirally thickened tracheids forming the apex of the protoxylem ridge. The occurrence of this groove is relatively infrequent and is, in no sense, a characteristic feature of the trace. I am thus in agreement with the description of Surange who correctly describes the character and position of the protoxylem. The narrower metaxylem tracheids show scalariform thickening. Most of the metaxylem, however, the tracheids of which are much larger in diameter than those of the stem, possess two or more rows of transversely elongated pits (Pl. 58, fig. 1). Occasionally, traces of the phloem and its associated parenchyma are preserved but these are usually too small in amount to yield much information. The best preserved example so far discovered is that illustrated in Pl. 58, fig. 4, in which a strip of sieve tubes and phloem parenchyma occurs on the abaxial side of the vascular bundle. The endodermis consists of small, tangentially flattened thin-walled cells devoid of thickening and which may have dark contents. The inner cortex consists of parenchymatous cells, some of which may have been secretory in character. The latter are distributed singly through the rest of the parenchyma and are distinguished by their brown contents (Pl. 58, fig. 5). They bear a close resemblance to the mucilage-secreting cells commonly occurring in the cortex of many existing ferns. The cortical cells diminish in size towards the exterior and, in mature petioles, these smaller cells develop thickened walls and form a well-defined sclerenchymatous outer zone. The small-celled epidermis shows no specially distinctive features, apart from the uniseriate surface hairs developed at and near the bases of the petioles. The branching of the petiole follows no set pattern and the examples figured by Surange (1952) adequately illustrate its general character. The branches undergo progressive diminution in size and may undergo, occasionally, equal bifurcation near their junction with a branch of a higher order, as in the example shown in Pl. 60, fig. 5.

Associated with the vascular bundles which supply the petioles are much smaller monarch traces supplying the organs which Benson termed aphlebiae and which she described as uninerved sheathing organs. According to her, the monarch petiolar bundles " apparently never come off (*from the stem stele*), pass through the cortex and enter the petiole without being accompanied by aphlebiae ". Surange, although describing and figuring one of these small monarch bundles as being given off from the stem stele immediately following the emission of the first petiole trace (Surange, 1952, text-fig. 1, *c–f*) does not record or figure them as constantly accompanying subsequent petiole traces. The sections studied during the present investigation do not support the view that they accompanied all, or indeed the majority, of the petiole traces. Where they are present, their relation to these traces is very variable and the two examples figured here show a wide divergence in their point of origin from the stem stele. The first, illustrated in Pl. 56, fig. 1 and Text-figs. 1–3, arises quite independently as a small endarch trace between the first and second of the petiole traces figured and is approximately equidistant between them. It ultimately supplies a small outgrowth of the stem which is ovoid in transverse section with the flatter side adaxial. The two examples illustrated by Benson (1911, text-figs. 1*a*, *b*) appear to supply similar outgrowths. Both are from thick and somewhat poorly preserved sections but that shown in her text-fig. 1*a* clearly shows the beginning of the ovoid shape in transverse section which is assumed when the " aphlebia " becomes free from the stem cortex. The second example (Benson's text-fig. 1*b*) appears to be more closely associated with an outgoing petiole and has an irregular shred of cortical tissue linking it with this. As in her text-fig. 1*a*, there are indications that, in this example also, the " aphlebia " was ovoid and not winged in transverse section.

The second example figured in the present paper is one in which the vascular bundle destined for the petiole and that destined for the small monarch trace arise simultaneously from the stem stele and are initially completely fused. As the petiolar trace passes into the stem cortex the small bundle becomes independent and diverges from the larger one though it accompanies it into the petiole (Pl. 56, figs. 1, 2). Whether this bundle should be interpreted as an abortive " aphlebia " or a precocious branch of the petiole is a matter of opinion. It should be pointed out, however, that a complete series exists ranging at the one extreme from a strand arising from the stem stele without any obvious connection with that supplying the nearest petiole to that just described in which the linkage between the two is close and prolonged.

Whatever the interpretation of the morphological nature of the structures supplied by these strands may be, they differ widely from the type of structure to which Solms-Laubach (1891) applied the descriptive name " Aphlebia ". This was applied by him to a distinctive and anomalous type of pinna or pinnule possessing a reduced and deeply dissected lamina which occurred on the rachises of certain fossil ferns and pteridosperms. These were compared by him to similar pinnae present in *Hemitelia capensis* and other existing ferns. Subsequent authors have applied the name to the scale-like structures occurring on the stems of several of the zygopterid ferns and to the somewhat similar pinnules borne on their petioles (Potonié, 1903 ; Seward, 1910 ; Bertrand, 1911 ; Gordon, 1911 ; Scott, 1920). This extended use of the name " Aphlebia " does not appear to serve any really useful purpose and it would seem preferable to limit it to the type of structure to which Solms-Laubach originally applied it.

The Diarch Axes

In addition to the monarch petioles, there were other, generally stouter, axes possessing two adaxial protoxylem groups, which were obviously parts of the same plant. These, as already stated, were regarded by Benson (1911) as diarch petioles but have been interpreted provisionally by Surange (1952) as dorsiventral stems from which the radially organized plants arose. We owe the detailed description of the development of these radially organized plants from the diarch axes to Surange and, apart from minor details, there is little to add to his account of the specimens he studied. A typical specimen, cut obliquely and showing two stages in the formation of a radial stem, is illustrated in Pl. 56, figs. 3, 4. It is evident that Benson's material was inadequate for a similarly detailed study and this led her to misinterpret the sections figured in her paper as " successive transverse sections through a stem stele " (Benson, 1911, pl. 81, figs. 1–5).

Re-examination of the relevant slides in the Benson Collection leaves little doubt that they represent part of a diarch axis from which a radial stem is developing. The section figured by Kidston (1908, fig. 11) and described by him as that of a petiole showing an early stage in petiolar dichotomy is also probably one of a diarch axis showing an early stage in the development of a radial stem.

Whilst, however, both the Benson and Kidston specimens described above fit without difficulty into Surange's interpretation of the behaviour of the diarch axis this interpretation is unsatisfactory when applied to the specimen figured by Benson (1911, pl. 82, figs. 11–13, 11*a*–13*a*). In the sections from which this series of figures has been made there is no indication that the diarch axis has divided into two monarch daughter axes, one of which is destined to be the source of a radial stem. The figured sections are interpreted by Benson as " a series through a stem bearing at first a diarch trace and later roots ". She also states that " the series shows diagrammatically the change in character of the stem as it passes from a purely leaf-bearing zone into a root-bearing zone ". The sections upon which this interpretation is based are the second, third and fourth of a series of five slides numbered 417·1 to 417·5, figs. 11 and 11*a* showing the stage present in 417·4, figs. 12 and 12*a* that present in 417·3 and figs. 13 and 13*a* that present in 417·2. Of the two remaining slides in this series 417·5 shows no substantial change from that in 417·4 and 417·1 has been shattered during grinding. A comparison of Benson's pl. 81, fig. 2 with her fig. 11*a* shows that these are essentially similar and it is suggested that both represent an early stage in the development of a radial stem. Whereas, however, the plant illustrated in her figs. 1–5 fits in with Surange's account of the behaviour of the diarch axis that illustrated in the 417 series clearly differs since the radial stem originates on one side of this axis without involving its division into two monarch daughter axes.

In addition to the Benson Collection specimen, there is a relatively short series of " peels " in the author's collection which presents some difficulties of interpretation when considered in connection with Surange's views. This series consists of ten transverse sections numbered H.96 and H.103 to H.111 and ten longitudinal sections through the base of the specimen numbered H.112 to H.121. A typical transverse section shows a well-developed diarch axis linked with the stem by its cortical tissues (Pl. 59, fig. 1). The stele of this axis unites with that of the stem at a lower level and is well shown in slide number H.115 (Pl. 59, fig. 2). This slide, owing to the curvature of the specimen, shows the axis and the stem partly in transverse and partly in longitudinal section. The stem stele is clearly radial in type but the series is unfortunately too short to yield any information as to its origin. On the opposite side of the stele to that at which fusion with the diarch axis has occurred there is a large developing lateral trace occupying almost two-thirds of the area of the stele. The stem cortex consists almost entirely of thick-walled cells and only towards the lower transverse sections is there any indication of root development though at this level two root traces are coming off in close juxtaposition. Whether or not this specimen is one of a stem from which two successive diarch axes have been produced must be an open question but if this interpretation is accepted it provides some support for the view put forward by Benson as to the plant being heterophyllous. It certainly differs to a marked extent, both in the nature of its cortical tissues and in its stelar characters, from a typical radially organized stem.

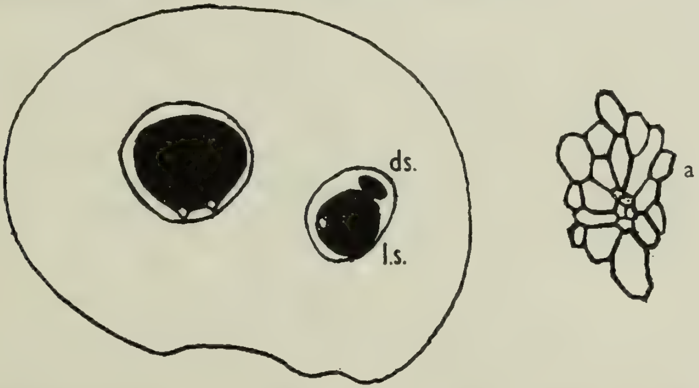


Fig. 8. Camera lucida outline of a diarch petiole in transverse section which has given off a lateral strand (*ls*) and which in its turn has given off a daughter stele (*ds*). Fig. 8*a*, Daughter stele, × 150. B.M. (N.H.) Oliver Coll. 1272.

An additional and different type of behaviour is also shown by some diarch axes which produce lateral branches having no apparent connection with radial stem formation. Benson (1911 : 1048) refers to a specimen of this kind (Benson Collection, Series 390) and figures an early stage in the formation of such a lateral branch (pl. 83, fig. 24). These branches are initiated by the division of one of the two protoxylem groups of the diarch axis following which the outer protoxylem group, together with its associated metaxylem, separates off to form the branch trace. Three of the stages in the formation of such a branch are illustrated in Pl. 57, figs. 4–6, from slides in the Oliver Collection. In an additional section at a stage similar to that in Pl. 57, fig. 6, the lateral trace has, in its turn, developed a small, somewhat irregular group of tracheids on its abaxial side which suggests that it may be possibly an early stage in the formation of a stem (Text-figs. 8, 8*a*). Any firm view as to its significance, however, is impossible on the evidence of an isolated section and it is figured here primarily to record its existence.

The specimens studied by Surange (1952) gave no clue to the origin of the diarch axes and it was clearly important to ascertain this, if possible, before any assessment could be made of their morphological status. Before attempting this, however, it seemed desirable that a review of the evidence upon which Surange had based his interpretation should be made. He, himself, realized that he had to rely on the criteria provided by comparative anatomy and that the acceptance of his view presented certain difficulties. Some of these, such as the pseudocollateral vascular structure, the possession of tracheids of wide diameter similar to those of the monarch petioles and differing from those of the radial stem and the fact that the axes do not appear to develop either petioles or a root system, were noted by him. In support of his view, however, he points out that among the Hymenophyllaceae the stems of certain species such as *Hymenophyllum sericeum* possess a pseudocollateral type of vascular structure closely resembling the condition present in the diarch axes of *Botryopteris antiqua*. It is doubtful, however, how much weight can be given to this comparison since *Hymenophyllum sericeum* is one of a series of filmy ferns in which there is a progressive reduction in the amount of vascular tissue this consisting, in the ultimate members of the series such as *H. tunbridgense*, of a minute pseudocollateral monarch strand (Boodle, 1900 ; Tansley, 1908 ; Ogura, 1938).

There does not seem to be any evidence that *Botryopteris antiqua* was a species in which reduction of the vascular system had occurred and it is suggested that a study of the anatomy of the stem and leaf stolons characterizing certain living ferns would provide a closer analogy with the diarch axes of *B. antiqua* than that used by Surange.

Among the ferns developing stem stolons those which have been most extensively studied are various species of *Nephrolepis* (e.g. *N. exaltata*, *N. cordifolia*, *N. neglecta*) (Lachmann, 1885, 1889 ; Sperlich, 1906 ; Sahni, 1916) but Bower (1923, 1926) also records their occurrence in *Plagiogyria pycnophylla* and *Thyrsopteris elegans*. In all these ferns the symmetry of the vascular supply of the stolon is radial in type and, initially at least, is a simplified version of that of the stem of the parent plant. The ferns in which flagelliform leaf stolons are developed are among those which have been investigated by Kupper (1906) in his comprehensive study of the formation of sporophytic buds on the leaves of ferns. Among these there is a group of related species of small fern belonging to the genus *Asplenium* namely *A. obtusilobum* Hk., *A. lauterbachii* Christ and *A. mannii* Hk. The first of these three species in addition to the normal leaves produces a series of transitional forms showing progressive reduction in the number of pinnae (Text-figs. 9*a*, *b*) the ultimate members being flagelliform stolons in which no pinnae at all are produced. These stolons and the modified leaves in which the pinnae are reduced develop sporophytic buds at intervals and are apparently of unlimited growth. Material of *A. obtusilobum*, a species from the New Hebrides, and of *A. lauterbachii*, from New Guinea, was not available for study but through the good offices of Mr. N. C. Chase of Umtali, Southern Rhodesia, a good supply of *A. mannii* was obtained. The specimens were collected from the North Range of the Vamba Mountains where it grows as an epiphyte on the boles and branches of forest trees. These plants, in addition to the normal leaves, bear flagelliform stolons (Hooker, 1854) on which sporophytic buds in various stages of development are produced, the longest of these in the material sent by Chase measuring 35 cm. and bearing ten attached plantlets (Text-fig. 9*c*). It is hoped to make a detailed investigation of this species later but, in connection with the present paper, attention has been concentrated on the morphology of the bud-bearing stolons. The vascular supply of these stolons consists of a somewhat strap-shaped xylem strand surrounded by phloem and phloem parenchyma with a protoxylem group occupying each extremity of the trace (Text-fig. 10*a*). When a sporophytic bud is to be formed one of the protoxylem groups accompanied by a small amount of metaxylem is detached from the rest of the leaf trace and becomes linked with the vascular supply of the developing sporophyte (Text-figs. 10*b*, *c*). This condition appears to furnish a close parallel to the behaviour of the vascular bundle in the diarch axes of *Botryopteris antiqua* and suggests that, applying the criteria of comparative anatomy, these

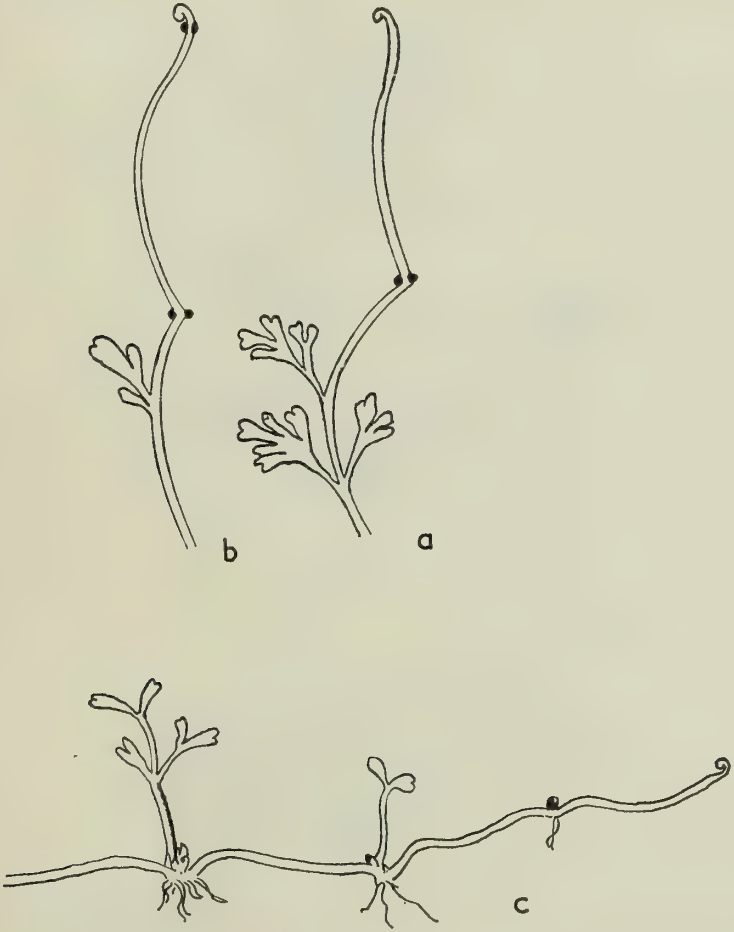


FIG. 9. *a*, *b*, Two leaves of *Asplenium obtusilobum* showing progressive pinna reduction and the formation of sporophytic buds. *After* Kupper, 1906. *c*, Part of a leaf stolon of *Asplenium mannii* showing three developing plantlets. All nat. size.

would be more accurately interpreted as specialized petioles rather than as dorsiventral stems. Whilst, however, on the criteria provided by comparative anatomy, there seem to be reasonable grounds for interpreting the diarch axes as petioles rather than stems it was considered that a search for specimens showing their origin was essential and several of the slides in both the Oliver and Gordon Collections yielded useful information in this connection. Two of the slides from the Oliver Collection (Pl. 57, figs. 2, 3) are from consecutive sections numbered 1263 and 1264 and show two successive stages in the departure of a typical diarch strand. This diarch strand and that illustrated in Text-fig. 11*a* arise from stems which appear to be radial in

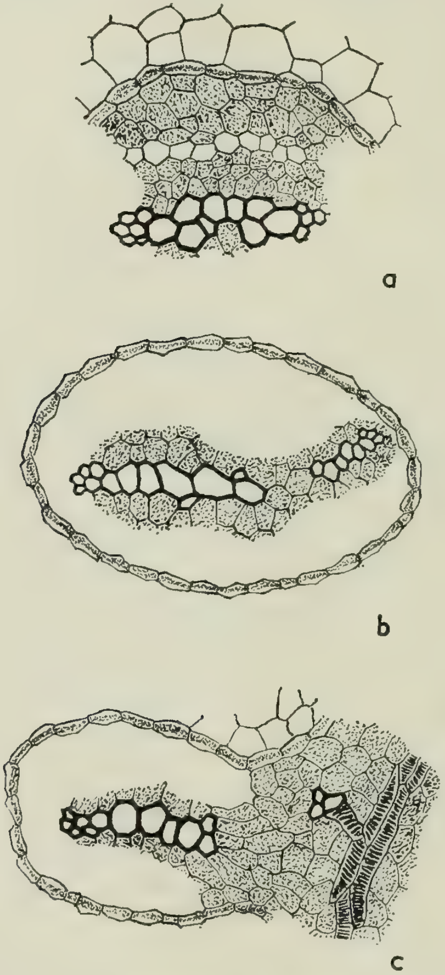


FIG. 10. Transverse sections of a leaf stolon of *Asplenium mannii* showing the development of the connection between the vascular bundle of the stolon and that of the sporophytic bud. × 170.

type. That these are, in fact, successive stages in its departure is shown by an examination of the next slide in the series (No. 1265). The stem and petioles in this slide are badly disintegrated but the xylem of the stem stele is intact and in it the differentiation of the xylem is still incomplete. It is interesting to note that this stem does not show a close succession of spirally developed monarch strands. In the section shown in Text-figs. 11*a*, *b*, however, a much smaller double vascular bundle has come off from the stem stele almost at right angles to that from which the diarch strand has arisen. This smaller bundle appears to be the vascular supply of a monarch petiole and is composed of two unequal endarch xylem groups (Text-fig. 11*b*). It bears a close resemblance to those strands already described in which the main petiolar strand is accompanied by a smaller accessory strand. Of the three slides from the Gordon Collection which are figured, two (Pl. 57, fig. 1 and Pl. 58, fig. 3) show a large diarch strand, with two mesarch protoxylem groups, lying in close proximity to the radially organized stem stele. In the third (Pl. 56, fig. 2) a similar

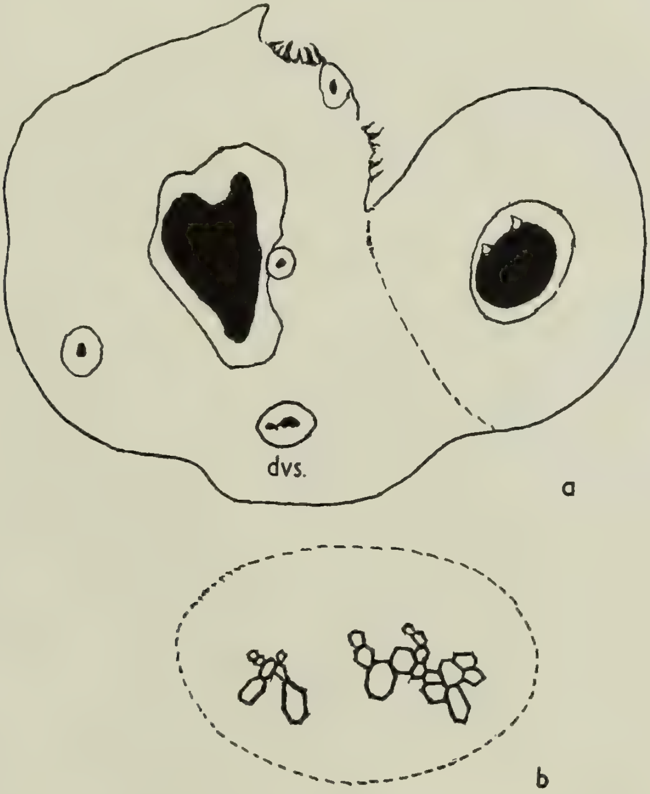


FIG. 11. *a*, Camera lucida outline of an oblique stem section showing an attached diarch axis and a small double vascular strand (*dvs*); *b*, the double vascular strand more highly magnified. B.M. (N.H.) Oliver Coll. 1274. *a*, ×30; *b*, ×150.

large diarch strand with mesarch protoxylems is dividing into a larger and a smaller bundle though these are still united. They show a pronounced difference from those cases in which a monarch petiolar strand is associated with a much smaller one. It is suggested that the dividing mesarch strand in this Gordon specimen may represent an unusually early division of the diarch axis prior to the formation of a radial stem from the smaller bundle. Like the specimens from the Oliver Collection, none of the Gordon specimens shows any indication of a close succession of spirally arranged monarch petioles.

It would seem fair to sum up the evidence as to the nature of the diarch axes by stating that the data provided by comparative anatomy and the evidence yielded by newer discoveries among the specimens of *Botryopteris antiqua* itself favour the interpretation of the diarch axes as petioles and that their development leads to a pronounced modification in the emission of the monarch petiole traces though there is no convincing evidence that the monarch and diarch petioles were developed in alternating series.

The Root System

The adventitious root system is mainly composed of slender diarch roots which show a close measure of structural agreement with those of existing leptosporangiate ferns. They possess a separate cortex from their point of origin with the stem stele and, in this region, the xylem is bulkier than it is in the more distal parts thus forming an expanded base of attachment (Pl. 56, fig. 2). The phloem and its associated parenchyma and most of the parenchymatous inner cortex are seldom preserved. In the few cases where it has survived petrifaction the inner cortex has, scattered through it, an irregular ring of cells with dark contents similar in type to those present in the inner cortex of the petiole (Pl. 56, fig. 3). The endodermis, also like that of the petiole, is formed of small tangentially flattened cells which often have dark contents. The outer cortex consists of thick-walled cells, smaller than those of the inner cortex, these forming a zone several cells in depth (Pl. 56, figs. 3, 4). As a rule, the surface layer of the roots has been eroded but even when this has survived no evidence has been found of the existence of root hairs.

In addition to the roots of the type just described, there are others which appear to be most abundant towards the stem apex and which show pronounced morphological differences from these. The evidence for the existence of this second type of root was initially somewhat unsatisfactory as their morphology was obscured by partial collapse and distortion. Happily, among the plants from a block in the Hemingway Collection a stem occurred which had developed a number of uncrushed roots thus enabling their salient features to be determined. There appears to be no doubt that these organs are roots since, like those already described, they possess their own cortex from the time of their inception and their xylem consists of a small diarch plate with an exarch protoxylem group at each end (Pl. 60, figs. 2, 3). The stele is relatively small and is surrounded by a wide cortex composed entirely of parenchyma, the cells of which have dense finely granular contents especially in the immature region near the apex (Pl. 60, figs. 1, 2). The surface layer is formed of dark flattened cells in which no detailed structure can be discerned (Pl. 60, figs. 1–3).

Any attempt to indicate the function of these roots must be somewhat speculative although their origin near the upper end of the stem and their morphology both suggest the possibility that they may be aerial and perhaps assimilatory in character.

Sporangia and Spores

Our knowledge of the sporangia and spores of *Botryopteris antiqua* is the least satisfactory part of the information available about this Lower Carboniferous plant though one can assign these to it with some degree of probability. The most satisfactory evidence yielded so far is that produced by Surange though even this is by no means conclusive. Commonly associated with the stems and petioles are sporangia with a multiseriate annulus, some of which contain well-preserved and quite distinctive spores. These sporangia are apparently borne on slender, branching axes each of which is traversed by a delicate vascular strand and the epidermis of which is characterized by dark cell contents. These have contracted away from the cell walls in many instances giving them a readily recognized appearance, especially in surface view (Pl. 60, fig. 6). The slender branches are closely associated with small branches of *Botryopteris antiqua* petioles which also often have epidermal cells with dark contents (Pl. 60, fig. 7). The spores contained in the sporangia are triangular in plan and are somewhat flat with trilete rays extending about three-quarters of the way towards the margin of each radius. They are smooth-walled and devoid of any ornamentation. The radial extremities are rounded and the interradial margins are concave. In proximal view the spores show a narrow raised margin but when seen from the distal side they show three large equal lobes surrounding a central triangular depression which leads to a flat, partly enclosed, central area (Text-figs. 12*a*–*c*). They are identical with those filling the sporangia which Scott (1910) figured and described and which he regarded as possibly those of *B. antiqua*.

Careful and detailed descriptions of palaeozoic spores are a relatively recent feature of palaeobotanical studies and already palynology has produced a considerable specialized literature with regard to them. The earliest reference to spores with a triangular contour which has been traced so far is one by Renault (1896). His figure 17 shows a sporangium termed by him *Hymenophyllites β* in which most of the spores are spherical but in which there are also some spores which are triangular (*trigones*). In Renault's view (1896 : 20) it is probable that this appearance is due to a partial desiccation of the spores.

Recent investigations, however, have shown that subtriangular types of spore occur quite commonly among palaeozoic spore assemblages. Among these Kosanke (1950, pl. 3, fig. 4) illustrates a spore of this kind to which he has given the name *Granulosporites concavus*. This has rounded corners, is smooth-walled and has strongly concave margins between the radii. Mamay (1950) also lists a species, *Botryopteris illinoensis*, which, like Kosanke's material, is from the Pennsylvanian of Illinois and in which the spores are described as " axially flattened, triangular, with concave sides " (Mamay, 1950, pl. 2, fig. 9).

These spores are from more recent geological strata than that in which *Botryopteris antiqua* occurs but spore assemblages from parts of the Scottish Lower Carboniferous have recently been investigated by Butterworth & Williams (1958) and by Love

(1960). Both these authors have described isolated spores which appear to show a close resemblance to those associated with *B. antiqua*. These were assigned by Butterworth & Williams to the genus *Granulosporites* as *G. politus* but by Love to *Leiotriletes politus*. Love very kindly loaned to the Department of Palaeontology a " single spore " slide of his *Leiotriletes politus* for comparison with the spores present in the sporangia from the Calciferous Sandstone and this has established beyond reasonable doubt that this spore and the spores from the petrified sporangia are identical.

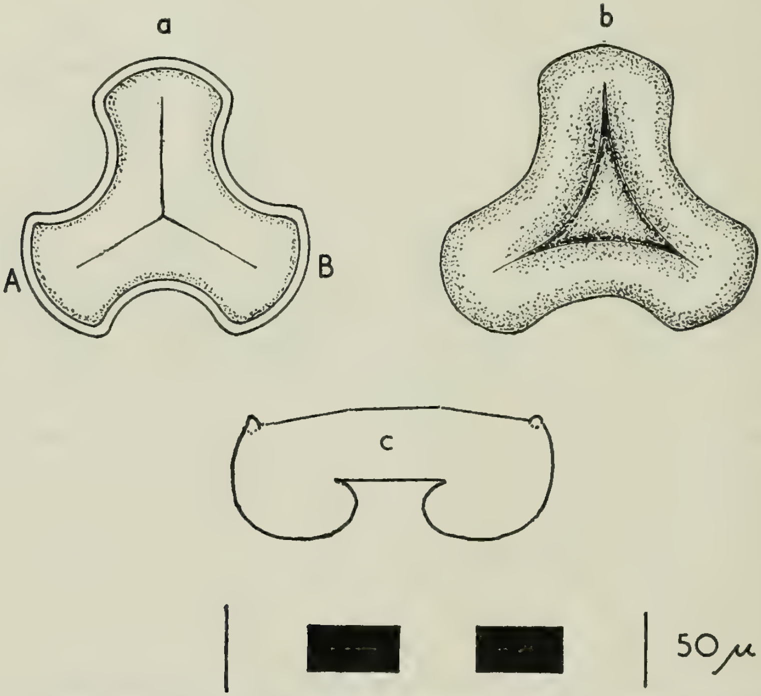


Fig. 12. *a*, Proximal and *b* distal appearance of trilete spores ; *c*, section of spore along plane A, B, of 12*a*. *a*, Surange Coll. B.154 ; *b*, Surange Coll. B.70

The evidence for the assigning of these sporangia and spores to *Botryopteris antiqua* is obviously not conclusive and it is hoped that proof of their relationship will be furnished when suitable specimens are available.

Neither Kidston, Benson nor Surange have attempted a formal diagnosis of *Botryopteris antiqua* and the following is suggested as covering the known data :

Botryopteris antiqua Kidston

Diagnosis. Small palaeozoic fern. *Stem* radially organized, protostelic with wholly tracheidal xylem, narrow scalariform tracheids forming bulk of stele, often wider tracheids with two or more rows of transversely elongated pits developed peripherally;

protoxylem spirally thickened ; mesarch : cortex divided into parenchymatous inner and outer zones with sclerenchymatous middle zone ; epidermis, especially at and near stem apex, developing numerous unbranched uniseriate hairs forming a protective mantle over the apex and extending on to bases of petioles. *Petioles* oval in transverse section, monodesmic with initially mesarch protoxylem becoming endarch ; petioles of two kinds, one possessing a single adaxial protoxylem group, the other possessing two adaxial protoxylem groups ; monarch petioles developed in close spiral succession, branching repeatedly, sometimes accompanied by small endarch subsidiary vascular bundle ; diarch petioles often developing sporophytic buds giving rise to radially organized daughter plants and, when present, largely replacing monarch petioles. *Roots* diarch with separate cortex throughout. majority with sclerenchymatous outer cortex. A second type of root with wide, wholly parenchymatous cortex developed at and near stem apex.

Sporangia provisionally assigned to *B. antiqua* having a multiseriate annulus and containing subtriangular, smooth-walled and trilete spores with rounded angles and concave interradii.

LECTOTYPE.—A transverse section of a dichotomizing stem figured by Kidston (1908, fig. 6) bearing roots and a petiole. Kidston Coll., Glasgow University, slide 549*c*.

DISCUSSION

It is almost inevitable that the study of the morphology of any fossil plant is one which shows a progressive series of stages largely dependent on the number and quality of preservation of the specimens available to the investigator and, to a less extent, on the evolution of techniques which enable a better use to be made of those at his disposal. The series of morphological studies of *Botryopteris antiqua* including the present paper clearly exemplify this. Although the plant was first recognized and briefly described by Kidston the chief value of his paper was that it provided a basis for further study. Benson's work appreciably amplified our knowledge though the techniques then available led her to misinterpret some of the plant's morphological characteristics. Surange, applying newer techniques, has been able to correct certain of these misinterpretations and to make appreciable additions to our knowledge though some of his tentative interpretations have oversimplified the morphological problems involved. These three investigators have provided, however, a reasonably secure foundation for further work and it is considered that the present account simply marks an additional stage in the elucidation of the morphology of this palaeozoic fern. The most important feature about which additional information is desirable is definite proof that the associated sporangia are those of *Botryopteris antiqua*. More detailed knowledge of the behaviour of the diarch petioles would be welcome also. Their preservation mainly as comparatively short, isolated segments fails to give a clear idea of their complete morphology. This may be due to their being shed from the parent plant when mature or by their being parted from it by decay of the parts connecting one with the other. The radially organized plants to which they give rise vary considerably in size but this may well be due to the stage of development they have reached. They are obviously not terminal in position but the minute stele figured in Pl. 59, fig. 7, which, though fully differentiated, only measures 0·3 mm. in diameter probably developed from the distal part of the parent axis. Quite small petioles with steles having two symmetrically placed adaxial protoxylem groups are not uncommon but whether they represent the initial stage in the branching of a monarch petiole or the distal parts of a diarch petiole cannot be determined from isolated sections.

Botryopteris antiqua seems to fall naturally into place taxonomically among the European Coal Measure species of the genus though its petiolar anatomy is somewhat simpler. It shares with them a homogeneous protostele with mesarch protoxylem groups, the apex of which is protected by predominantly uniseriate unbranched hairs and a monodesmic petiolar vascular supply which retains the form of a tangentially compressed cylinder. It also shares with *Botryopteris hirsuta* the specialized type of petiole on which sporophytic plantlets are developed. Whether the genus *Botryopteris* as at present constituted is a natural one is perhaps open to some doubt. *B. forensis* and some of the American species such as *B. americana* (Delevoryas & Morgan, 1954) and *B. trisecta* (Mamay & Andrews, 1950) have much in common and show considerable differences from the European Coal Measure species and from *B. antiqua*. The best solution, if all are to be retained in the same genus, would seem to be the creation of separate subgenera for the two groups.

SUMMARY

Botryopteris antiqua is a minute fern occurring in the Scottish Lower Carboniferous.

The stem, which is radially organized, possesses a stele which has the shape of a shallow dome. It is protostelic with xylem which is wholly tracheidal and in which the protoxylem is mesarch. The xylem is enclosed by a continuous sheath of phloem and by a cortex differentiated into parenchymatous inner and outer zones and a sclerotic middle zone. The stem apex is overarched by a closely set system of unbranched and predominantly uniseriate hairs which extend on to the proximal parts of the petioles.

These are of two kinds, monarch with a single adaxial protoxylem and diarch with two adaxial protoxylem groups. The petiolar vascular supply is monodesmic and has the form of a tangentially flattened cylinder with the protoxylem forming either one or two adaxial ridges. The monarch petioles branch freely and are developed in spiral succession.

The diarch petioles are generally larger than the monarch ones and branch less frequently. They often produce sporophytic buds and their development interrupts the spiral development of the monarch ones.

The root system consists of diarch roots of two kinds, the majority having an outer zone of cortical sclerenchyma. In a second type of root the cortex is wholly parenchymatous.

Sporangia which are frequently associated with the stems and petioles have a multiseriate annulus and contain smooth-walled subtriangular trilete spores with concave interradii.

ACKNOWLEDGEMENTS

In addition to those whose help has been acknowledged in the body of the paper, the author is also greatly indebted to Dr. E. I. White, Keeper of the Department of Palaeontology, for facilities for studying the palaeobotanical collections in his charge, to Mr. F. M. Wonnacott for his expert help in many ways and to the staff of the Photographic Department of the Museum for their care and co-operation in the production of the negatives and prints from which the plates illustrating this paper have been made.

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PLATE 56

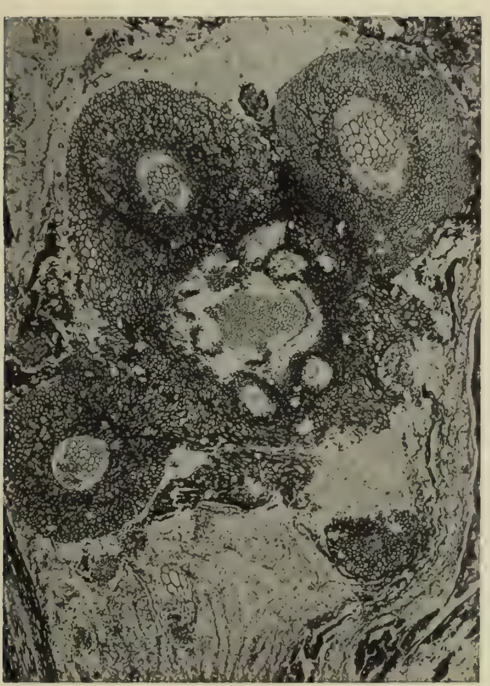
Botryopteris antiqua Kidston

FIG. 1. Transverse section of a stem showing stages in the emission of petioles and root traces. Note the sclerized outer cortex of the roots and, at the right bottom corner of the figure, one of Benson's " aphlebiae ". B.M. (N.H.) Holden Coll., No. H.152. × 12.

FIG. 2. Transverse section of stem in which the whole of the cortical tissues are preserved and which shows the emission of three roots and a dividing petiole trace with mesarch protoxylems. Gordon Coll., King's College, London. × 12.

FIG. 3. Oblique section of a dividing diarch petiole, the smaller branch of which is associated with the basal root-bearing part of a daughter sporophyte. Note the increase in the number of tracheids where the root steles join the parent stele. B.M. (N.H.) Holden Coll., No. H.152. × 12.

FIG. 4. Oblique section of the same plant as that shown in Fig. 3 but cut at a lower level and in which the daughter stem is well shown. B.M. (N.H.) Holden Coll., No. H.162. × 12.



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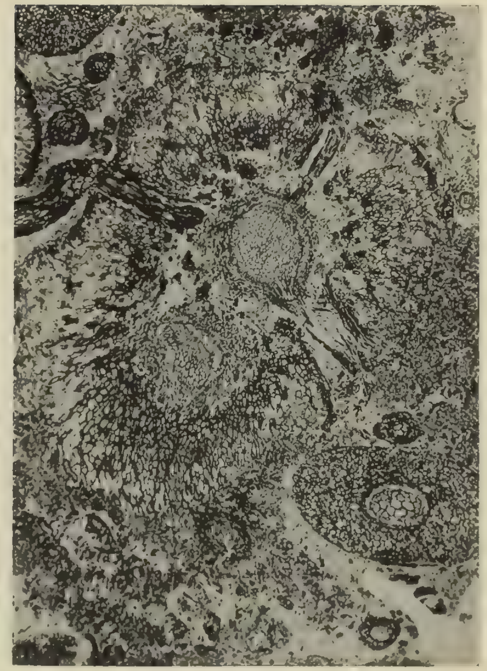

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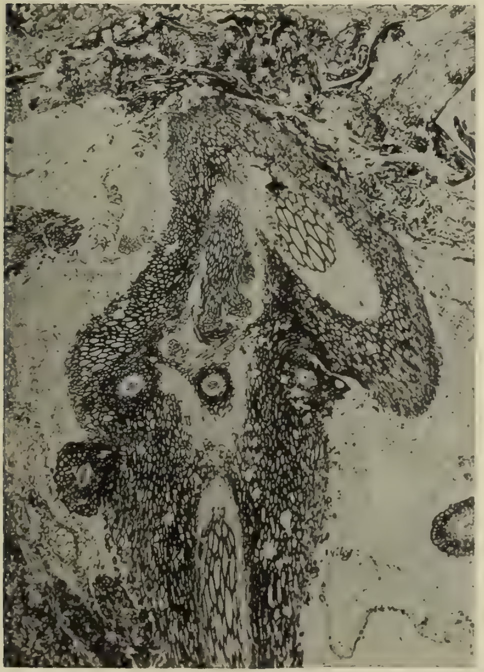

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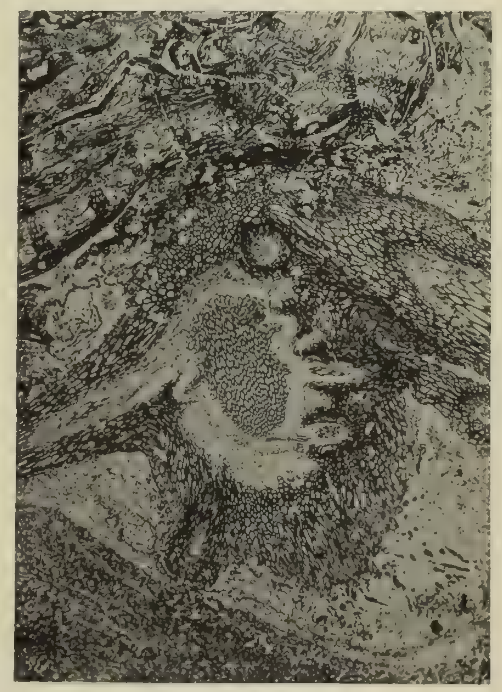

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BOTRYOPTERIS

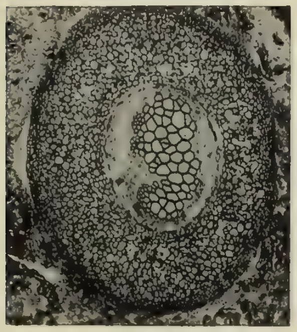
PLATE 57

Botryopteris antiqua Kidston

FIG. 1. Transverse section of a stem with a large mesarch petiole trace with two protoxylem groups. The cortical tissues are well preserved and the small-celled epidermis is clearly shown on the lower side of the figure. Gordon Coll., King's College, London. × 10.

FIGS. 2, 3. Transverse sections showing two stages in the emission of a diarch petiole. Fig. 2, B.M. (N.H.), Oliver Coll., No. 1263 ; Fig. 3, Oliver Coll., No. 1264. × 10.

FIGS. 4–6. Sections showing three stages in the emission of a branch trace from that of a diarch petiole. B.M. (N.H.) Oliver Coll., Nos. 1261, 1262, 1238 respectively. All × 15 approx.



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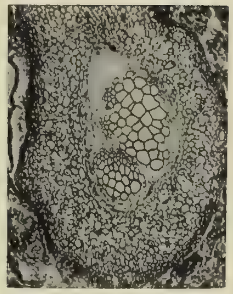

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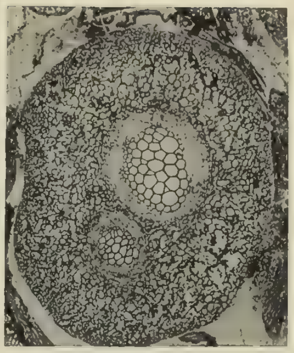

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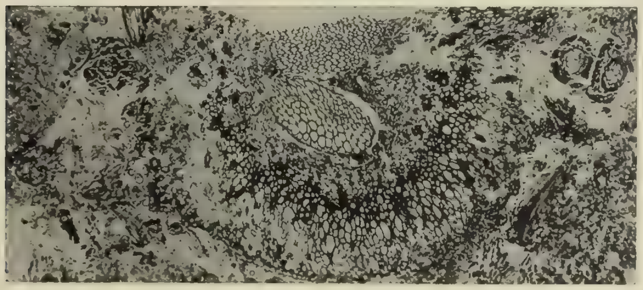

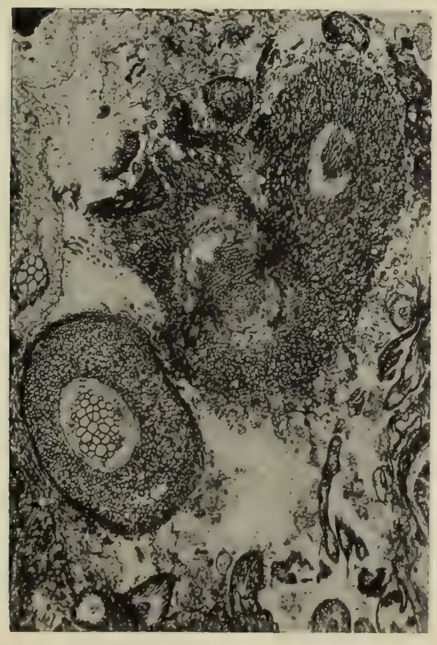

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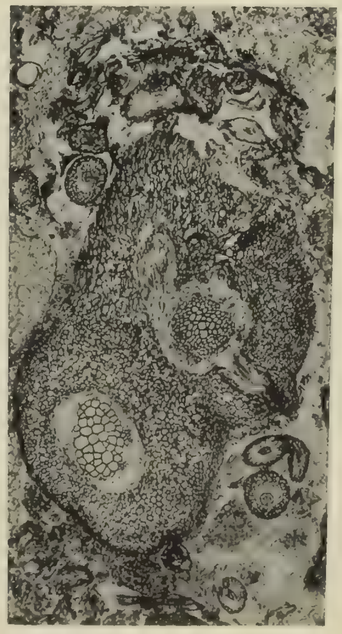

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BOTRYOPTERIS

PLATE 58

Botryopteris antiqua Kidston

FIG. 1. Longitudinal section of part of the xylem of a petiole showing the types of tracheidal pitting and the disruption of the protoxylem. Glasgow Univ. Figd. Slide Coll., No. 714. × 150.

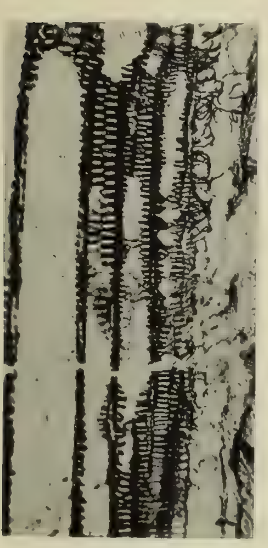
FIG. 2. Longitudinal section through the protoxylem of a petiole showing an early stage in the breakdown of the spirally thickened tracheids. B.M. (N.H.) Holden Coll., No. H.162. × 70.

FIG. 3. Transverse section of stem giving off a root trace and with a large petiole trace with two protoxylem groups to the left of the figure. Gordon Coll., King's College, London. × 16.

FIG. 4. Transverse section of a petiole showing a strip of sieve tubes on the abaxial side of the stele. Gordon Coll., King's College, London. × 35.

FIG. 5. Part of a petiole in both transverse and longitudinal section showing the cortical secretory cells. Surange Coll., No. B. 34. × 20.

FIGS. 6–8. Transverse sections of successive stages in the emission of a petiole trace and a subsidiary daughter trace. B.M. (N.H.) No. V.35555; Fig. 6, slide 73*b*; Fig. 7, slide 82*b*; Fig. 8, slide 86*b*. All × 20.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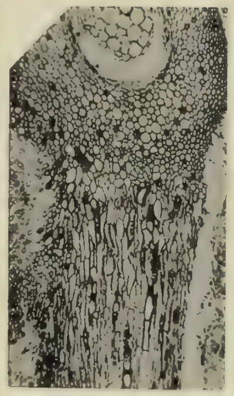
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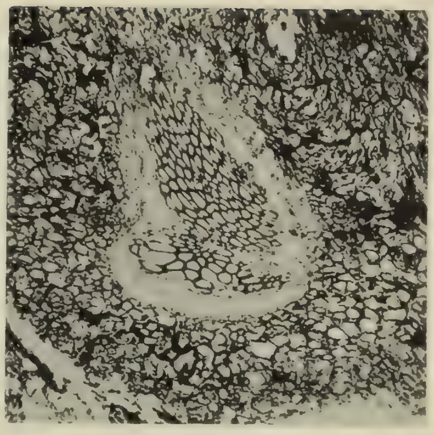
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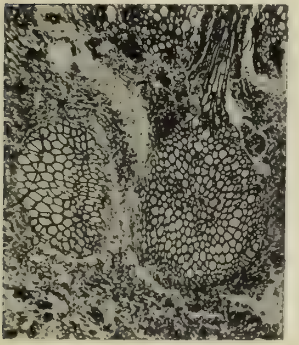
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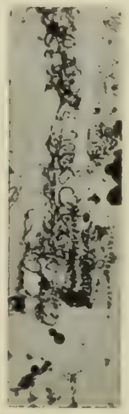
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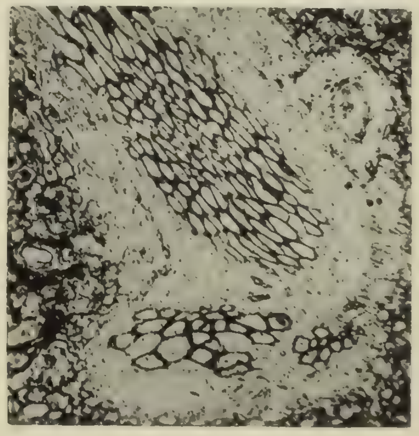
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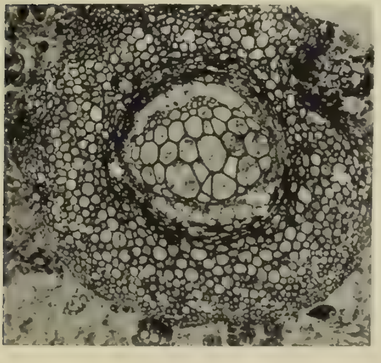
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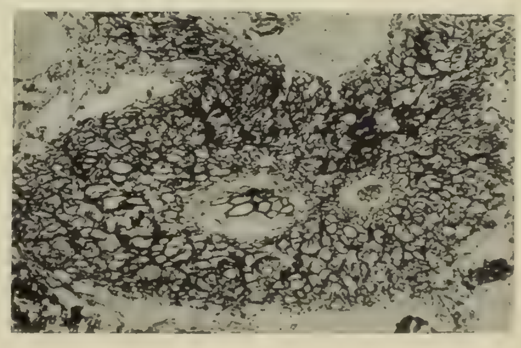
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BOTRYOPTERIS

PLATE 59

Botryopteris antiqua Kidston

FIG. 1. Transverse section of a stem with attached diarch petiole to the right and showing an early stage in the formation of a second petiole trace to the left. Note the character of the stem cortex. B.M. (N.H.) Holden Coll., No. H.101. × 16.

FIG. 2. The same stem cut partly in transverse and partly in longitudinal section showing the junction of the petiole trace with the stem stele. B.M. (N.H.) Holden Coll., No. H.115. × 16.

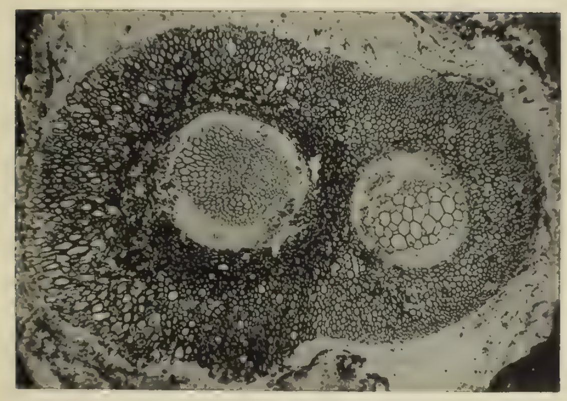
FIG. 3. Section through a stem showing a circinately coiled petiole and, to the right, parts of surface hairs. The small ringed group of xylem is much more highly magnified in Fig. 4. Surange Coll., No. B.78. × 20.

FIG. 4. Small group of tracheids showing a spiral protoxylem and a pitted metaxylem element. Surange Coll., No. B.78. × 700.

FIG. 5. Transverse section of an immature root still embedded in the stem cortex. Note the diarch xylem plate and the cortical cells with dark contents. Kidston Coll., Glasgow University, No. 670*c*. × 100.

FIG. 6. Transverse section of a stem stele near its apex showing incomplete differentiation of the xylem. Surange Coll., No. B.34. × 50.

FIG. 7. Transverse section of the stele of a very small stem in which the differentiation of the xylem is complete. B.M. (N.H.) No. V.35555, slide 3*b*. × 100.



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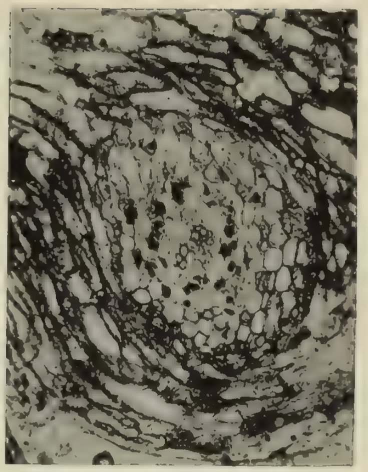

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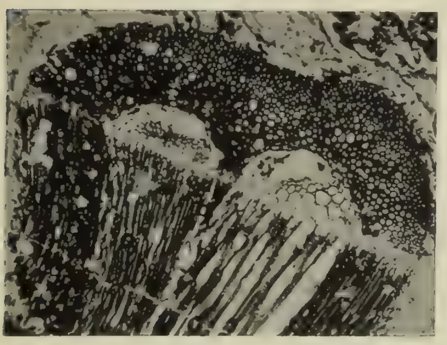

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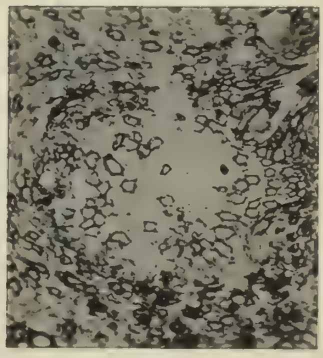

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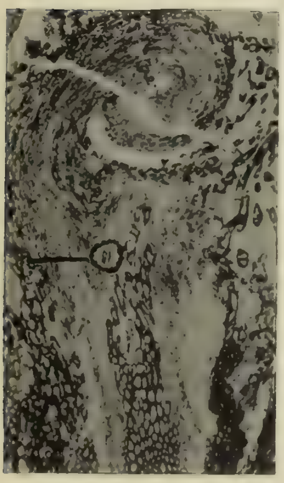

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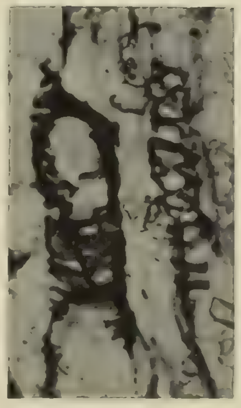

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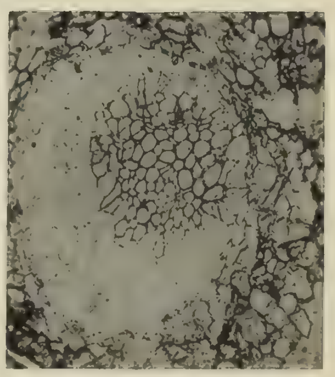

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BOTRYOPTERIS

PLATE 60

Botryopteris antiqua Kidston

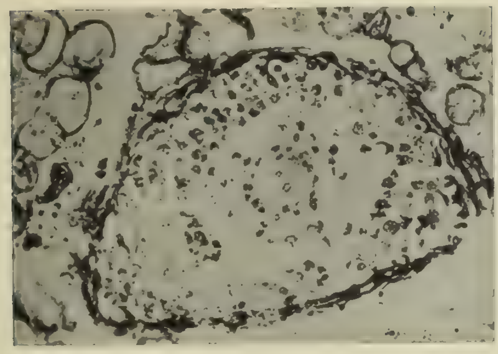
FIGS. 1–3. Successive stages in the differentiation of a second type of root. Note the dense contents of the cortical cells and the traces of surrounding hairs in Figs. 1, 2. B.M. (N.H.) No. V.35555. Fig. 1, slide 58*b* × 100 ; Fig. 2, slide 65*b* × 100 ; Fig. 3, slide 44*b* × 100.

FIG. 4. Transverse section of a petiole from Autun showing the characteristic adaxial concavity. Kidston Coll., Glasgow University, No. 2046. × 25.

FIG. 5. Transverse section of a branching petiole giving off two approximately equal daughter traces. Kidston Coll., Glasgow University, No. 1471. × 40.

FIG. 6. Minute sporangium-bearing branches. Note the dark cell contents of the epidermal cells and the subtriangular spore in the sporangium. Surange Coll., No. B.70. × 100.

FIG. 7. Tangential longitudinal section of a small branch giving off a still smaller branch. Note the dark epidermal cell contents. Surange Coll., No. B.33. × 80.



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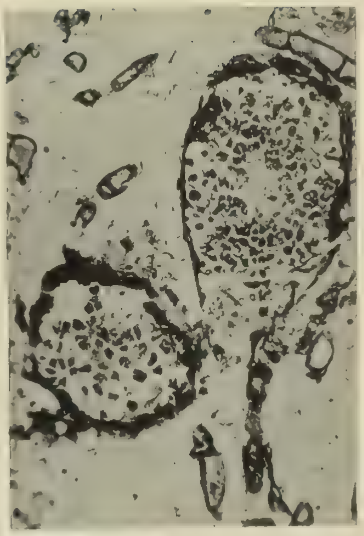

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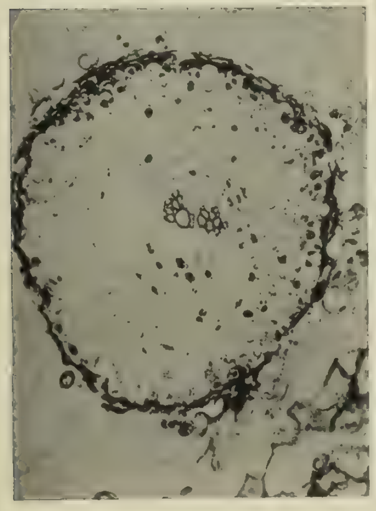

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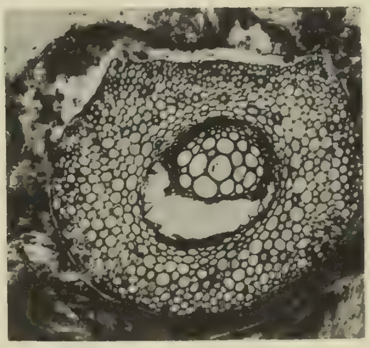

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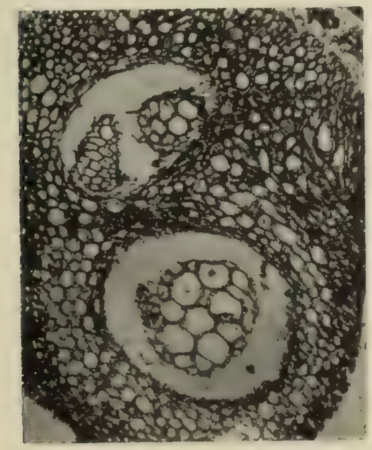

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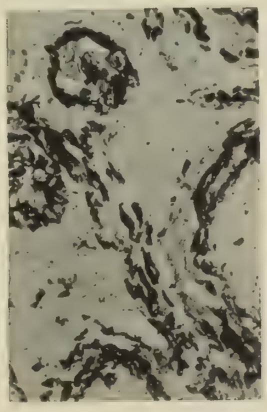

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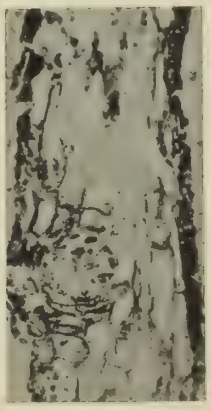

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BOTRYOPTERIS

BRITISH MUSEUM
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